The Effect of reduction of Predaceous Fish on survival of young Sockeye Salmon at Cultus Lake

By R. E. Foerster and W. E. Ricker
Pacific Biological Station

(*Received for publication July 16, 1940*)

ABSTRACT

By persistent gill-netting in Cultus lake, British Columbia, the predaceous fish which feed on young sockeye (*Oncorhynchus nerka*) have been considerably, though unevenly, reduced in numbers. The populations of squawfish and char, of lengths greater than 200 millimetres, were reduced in three years to about 1/10 of their original numbers. The abundance of trout and coho salmon have been much less affected by netting, if at all, though a considerable number have been killed. From the first year of control operations the survival rate of young sockeye salmon was considerably increased. In the three years which have been tested, the mean survival rate has been increased three and a third times over average conditions prior to control. In absolute figures, this represents 3,800,000 migrants saved, which are expected to yield 380,000 adult sockeye. Even disregarding the important cumulative future increase, the immediate return from the work is a quantity of sockeye whose value is many times greater than the cost of control work.

INTRODUCTION

In the course of the investigation of the propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus lake, B.C. (Foerster 1936b, 1938), it was discovered that large losses of young fish occur during their fresh-water life. From the time of egg deposition to that of the seaward migration of the young at one or two years of age, the percentage survival varied between 1.05 and 3.23 per cent, with an average of 1.80 per cent in three trials. When similar tests were made using fry hatched artifically, the survival rate was between 2.81 and 5.83 per cent, with an average of 4.16. It is evident then that a loss of roughly 96 per cent of the young salmon can be anticipated, even after they have hatched and emerged from the spawning beds.

As knowledge of the lake accumulated, it seemed probable that predaceous fish might be responsible for some of this loss. The fish of the lake were made the subject of special study, to ascertain what species might be considered predaceous upon sockeye, and to what extent. A summary of these studies is being presented in a separate paper (Ricker 1941). They show that squawfish, char, trout and, in a varying degree, coho salmon were the principal species in Cultus lake preying upon young sockeye.

From 1932 to 1934 a certain amount of exploratory gill netting was done and the catches studied. From 1935 to 1938 a systematic netting programme was undertaken, the objective being to test the effect of reduction in predaceous

J. Fish. Res. Bd. Can. 5 (4) 1941.

Printed in Canada

fish populations upon the survival of young sockeye in the lake. In the spring of 1938 the operations were taken over by the newly-formed International Pacific Salmon Fisheries Commission. The data pertaining to the 1938 net catches are included in this report with the kind permission of the Commission's Director of Scientific Investigations.

In the sections to follow the control operations are described, the results set down and the general significance of the findings discussed.

FISH REMOVED FROM THE LAKE

GILL-NETS

The fish taken from the lake were caught largely in gill-nets. The range of meshes used was as follows, the measurements being given as the "stretched" measure (between every other knot) in inches, with the equivalent in mm. in brackets: 5 (127), $4\frac{1}{2}$ (114), 4 (102), $3\frac{1}{2}$ (89), 3 (76), $2\frac{3}{4}$ (70), $2\frac{1}{2}$ (64), $2\frac{1}{4}$ (57), 2 (51), $1\frac{3}{4}$ (44), $1\frac{1}{2}$ (38), $1\frac{1}{4}$ (32), 1 1/16 (30), $\frac{7}{8}$ (22), $\frac{5}{8}$ (16). Of these, the two smallest were short hand-made pieces. Mesh 30 mm. was 46 metres long and 2.3 metres deep, when stretched. The other meshes, as used up to 1935, were nearly all 46 m. long and 1.8 m. deep. (A few nets 3.6 m. deep were made in 1935 by sewing two 1.8 m. nets together; and one net 10.7 m. deep and of 51 mm. mesh was used). In 1936 nets were obtained 2.7 metres deep, and in 1937, 3.6 metres deep, both in units 46 m. long; while in the latter year one net each of 57 and 70 mm. mesh was tried, 8.5 m. deep and 92 m. long. It was discovered, however, that nets deeper than 2.7 metres and longer than 46 m. caught few, if any, more fish than the smaller sizes.

In the years 1932 to 1934, nets were almost always set on the bottom of the lake in a long gang consisting of one net of each mesh used, usually 11 or 12 in all. The gang was placed at or near right angles to the shore, because numerous snags inshore made it impossible to set a long gang parallel to shore. As a result, most of the netting was in deep water, and the catch consisted predominantly of deep-water fish, chiefly char and, in winter, squawfish.

With the beginning of more intensive netting in May, 1935, changes were made in the manner of setting the nets. Instead of being joined into long gangs, most of the nets were set singly close inshore, usually with the shore end tied on the beach. In 1936 and 1937 a modification was introduced, using some of the deeper nets, by adding extra corks to make the cork-line float at the surface, with the mesh suspended below. Moderately long gangs of the larger meshes were still used in deep water during the summer of 1935 and 1936, however, to take char.

In table I the extent of the gill netting operations is shown. During 1932 to 1934 the netting was largely of an exploratory nature. Few nets of each mesh were used and for occasional nights only. In May, 1935, however, the programme was expanded and from then until October the number of nets was appreciably increased and the settings conducted fairly continuously. During 1936 a further increase in the netting occurred, particular attention being directed to the medium-sized meshes from 2 inch (51 mm.) to 3 inch (76 mm.). In 1937, the larger meshes, catching very little, were used but little, effort again being concentrated upon

TABLE I. Total number of net-nights of fishing, arranged according to mesh used, 1932 to 1938.

Mesh											Total
Inches	5	4½	4	3½	3	2¾	2½	2¼	2	1¾	1½	
Mm. .	127	114	102	89	76	70	64	57	51	44	38	
1932 . .	8	22	22	22	22	22	21	21	21	21	21	223
1933 . .	7	15	15	9	15	15	15	15	15	15	15	151
1934 . .	17	17	21	17	17	21	17	17	21	10	21	196
1935 . .	71	371	419	440	423	341	318	241	230			2,854
1936 . .		414	332	624	768	1390	1917	548	688	66	66	6,813
1937 . .		52	36	63	431	1508	1844	610	934		73	5,551
1938 . .		19	19	105	330	759	1004	761	461			3,458

medium meshes. Similarly for 1938, but here the data only embrace the netting operations from January to June.

The catches of fish in Cultus lake made by the gill-nets are summarized for each year in table II. Considerable variation occurs due to the variation in numbers of nets used, types of setting, etc., but these records indicate the general extent of the removal of predaceous fish from the lake during the netting campaign.

TABLE II. Catch of gill-nets, arranged by species, 1932 to 1938.

	Squawfish	Trout	Char	Coho	Sockeye	Whitefish	Chub	Suckers	Sculpins	Kokanee	Total of all species
1932	317	1	87	2	71	3	4	47	8		540
1933	109	4	22	0	6	1	1	7	1		151
1934	48	9	68	10	67	1	0	38	6		247
1935	2,046	225	232	44	72	17	8	853	42	13	3,552
1936	4,573	720	258	239	954	11	13	1,098	14	2	7,882
1937	1,783	764	177	268	21	4	1	900	227		4,145
1938	1,726	587	91	167	7	16	0	807	129		3,530
Total	10,602	2,310	935	730	1,198.	53	27	3,750	427	15	20,047

It was found that the gill-nets used were principally of sizes which would catch fish more than 200 mm. long. From the studies of stomach contents, it appears that squawfish and trout smaller than this (down to 150 mm. length or even less) do eat sockeye. Concerning char and coho below 200 mm., there is little information. However, the finer-meshed nets appeared to yield decreasing returns, and in any case removal of the larger predators was the first task to be faced.

OTHER METHODS

Other methods used to catch fish included seines, bait lines and cage traps. Seines were of 18 to 20 mm. stretched mesh, and usually 52 or 92 metres long. Used in summer and early autumn they caught 3,824 squawfish in 1935, 8,658 in 1936 and 6,416 in 1937; also a few hundred small trout and coho, 3,000 sculpins, 72,000 shiners and 24,000 sticklebacks. The squawfish taken were almost all less than 200 mm. long, and consisted predominantly of the year-old and two-year-old age groups. The bait lines and traps were used only in winter; they caught about two hundred squawfish and four hundred sculpins.

At the outlet of the lake are two fences, one designed to stop salmon migrants on their down-stream migration, the other to stop returning adults. Both catch

fish other than salmon at times, but as they have been in operation for many years, they do not constitute a *new* hazard for the lake's fish. The only point worthy of note is that in the spawning season 1934-35 only 140 female coho salmon were allowed to go above the adult fence, and most of these spawned near it instead of going into the lake. In that year the lake was very poorly stocked with young coho. Ordinarily 300 to 800 female coho appear, of which the majority spawn in the lake or its tributaries.

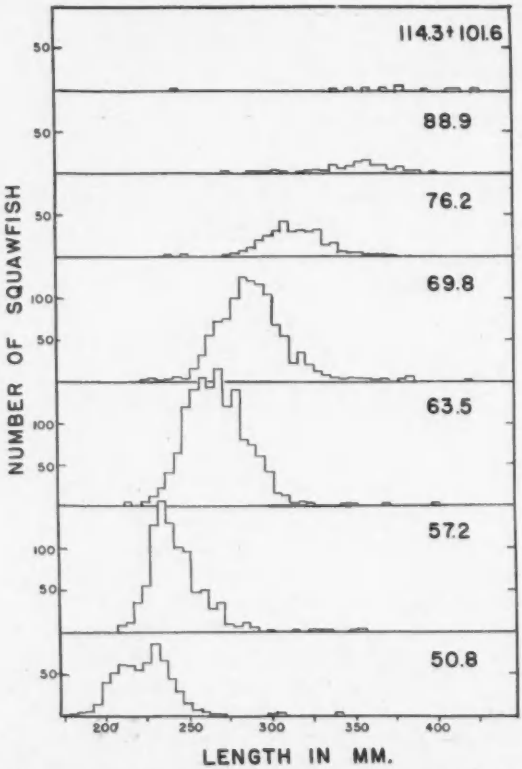

FIGURE 1. Length frequency distribution of all squawfish captured in gill-nets of various meshes (114 mm. or 4½", 102 mm. or 4", 89 mm. or 3½", 76 mm. or 3", 70 mm. or 2¾", 64 mm. or 2½", 57 mm. or 2¼", 51 mm. or 2") from March, 1936 to February, 1937.

CHANGES IN ABUNDANCE OF PREDATOR POPULATIONS

EFFICIENCY OF GEAR FOR VARIOUS SPECIES

Any change that may have been made in the abundance of various fish in the lake has been largely due to the gill-nets. Their effect on the different species in the different seasons is therefore discussed.

Squawfish were taken in largest numbers during the months of April, May, June and early July, in nets set near shore. This corresponded to their spawning

season, when they lay their eggs on the gravel beaches, often in quite shallow water. During most of July, August and early September, only very poor catches were made, in any kind of gear. Beginning mid-September, they became vulnerable to nets set on bottom off shore, and as the season advanced distributed themselves into even the deepest water. The fall fishery, however, did not catch as many per net as that of spring.

Char could be taken at all times of year, but appeared most vulnerable to nets set deep from June to August, and to shallower nets in September and October.

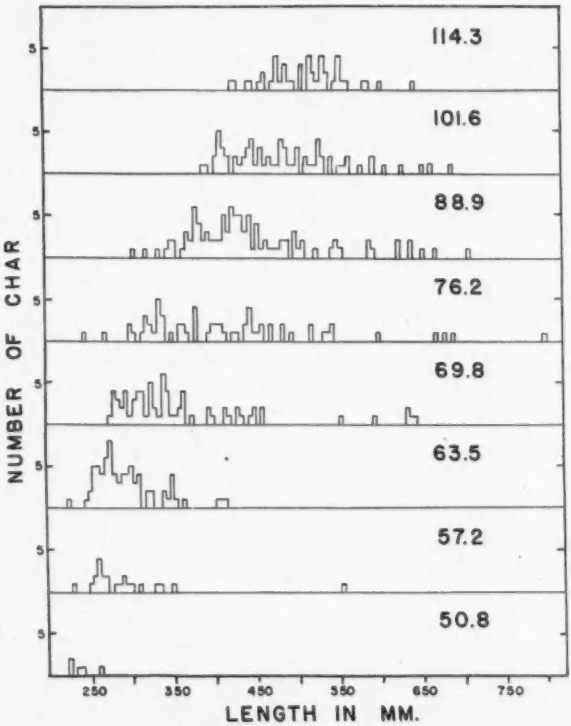

FIGURE 2. Length frequency distribution of all char caught in gill nets of various meshes (as in figure 1), from March, 1936 to February, 1937.

Trout also were vulnerable at all times of year, being taken most commonly in parts of nets lying near shore in summer, but not actually in the warm shore water, nor yet in the depths where char are commonest. Throughout the winter fair catches were made, and these became better as spring approached, particularly near the creeks at the south end of the lake.

Coho salmon were taken in approximately the same situations as trout, or possibly more commonly in slightly deeper water. They were not, however, taken in summer (June to September) in any numbers, with the gear used.

The choice of nets and types of sets used was in the main directed toward taking squawfish from the lake, these being the most numerous and least desirable of the salmon predators. For this purpose a concentration of gear in late April, May and June was used in years from 1936 on, and also from September to November in 1937, when no adult salmon were in the lake. In the summers of

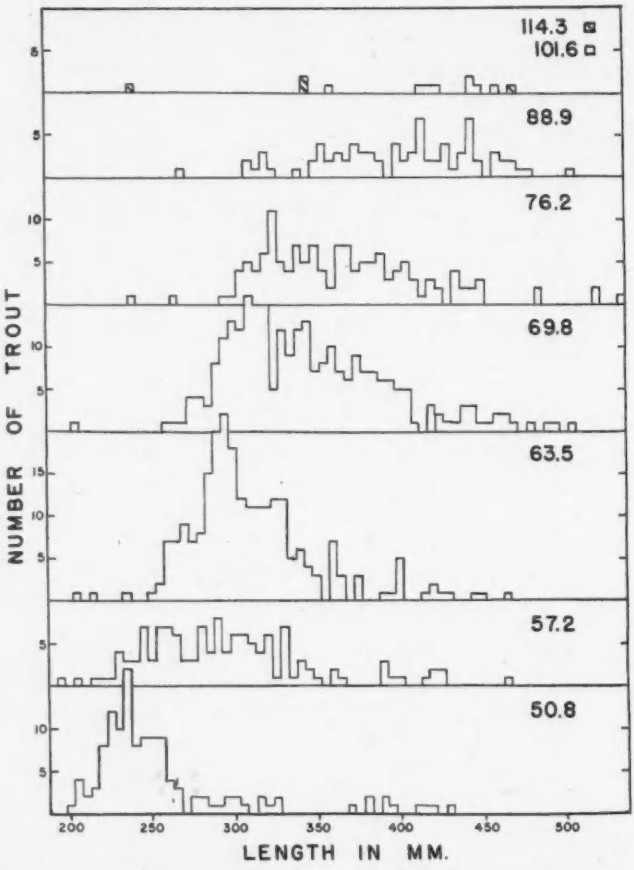

FIGURE 3. Length frequency distribution of all trout caught in gill nets of various meshes (as in figure 1), from March, 1936 to February, 1937.

1935 and 1936 a rather intensive deep-water fishery for char was maintained, but these fish became too scarce to permit its being profitably maintained in 1937. The early spring fishery (March and April) was largely for the purpose of removing squawfish, which, though not as readily caught then as later, are at that time taking their greatest toll of young sockeye. At the same time it took the even more destructive trout and coho salmon in some numbers.

Size of Fish Caught by Different Meshes

Figures 1, 2 and 3 give an idea of what size fish the various kinds of gear captured. For each mesh of gill-nets a normal range of gilling sizes is indicated which includes most of the fish captured by it. Outside of this range scattered individuals were taken, more especially of the salmonids. Some individuals became entangled by their teeth, not "gilled" in the proper sense. They were usually either larger or smaller than the normal size range, but more often larger. The bait lines used in the winter of 1935-36 caught squawfish of larger than average gill-net size, while those caught in cage traps were considerably smaller.

The three figures also give considerable information on the relative numbers of different size groups present in the lake, from about 200 mm. up, *during the periods covered.* It is shown later, however, that the different size groups present have changed greatly in numbers since netting was begun.

The largest fish ever taken by us in the lake, of each of the three species, were: squawfish 480 mm., trout 550 mm., and char 800 mm. Other maximum lengths are: sucker 500 mm., lake coho 595 mm.

Table III. Comparison of catches of nets set in identical manner and number, May 30–June 22, 1935, and May 26–June 18, 1938.

Mesh mm.	Year	Squawfish Catch	Squawfish Ratio	Trout Catch	Trout Ratio	Char Catch	Char Ratio
57	1935	256		8		6	
	1938	59	0.23	3	0.38	3	
64	1935	188		11		0	
	1938	9	0.05	1	0.09	2	
70	1935	313		26		9	
	1938	12	0.04	5	0.19	1	
76	1935	8		2		1	
	1938	0	—	4	2.0	0	
89	1935	10		0		1	
	1938	10	1.0	0	—	0	
102	1935	3		0		5	
	1938	8	2.7	3	—	0	
114	1935	4		0		0	
	1938	3	0.8	2	—	1	
All	1935	782		47		22	
	1938	101	0.13	18	0.38	7	0.32

Changes in Catch per Unit of Gear in Use

SQUAWFISH

Table III makes possible a direct comparison between the squawfish populations at the beginning of predator control and at its termination to date. For this test the conditions of fishing in late May and June of 1935 were duplicated in 1938 as regards the kind and number of nets set and the frequency with which they were tended and lifted. In order to make the total fishing effort the same in both years, all other netting operations on the lake were suspended. The 1938 population was only about one-eighth (0.13) of that of 1935, taking an average

over the size range covered by these nets. Within this range, greatest reduction was effected among fish of intermediate size: those taken in meshes 64 to 76 mm. being only 1/25 as numerous as formerly. The large fish taken by nets more than 76 mm. mesh were little if any scarcer, doubtless because these meshes were much less used than the smaller, in the last two years. The small fish taken in the 57 mm. mesh were 1/5 as numerous as in 1935, and it is probable that a 51 mm. mesh would have shown less reduction. These represent, of course, the young fish just entering the gill-net fishery of the type used.

A notable reduction in squawfish appears therefore to have been accomplished over the three-year period. Its progress during that time is less easy to trace. Between 1935 and 1936 there was a striking decrease in catch per unit of gear (80 to 95 per cent, table IV) calculated from May and June catches, but the large increase in gear used—at least ten times—makes it difficult to decide to what extent this is due to that fact, and to what extent it represents a real decline in abundance. In an earlier report (Foerster and Ricker 1938) the average decrease from June, 1935 to June, 1936 was rather arbitrarily estimated at 50%.

Between 1936 and 1937 there was not much change in the intensity of the June fishery, but the catch per unit again showed a marked decrease (table IV), averaging about 3/4 for meshes 64 to 76 mm. This is almost all to be attributed to decline in abundance. The 57 mm. mesh showed less decline (about 1/2), while the catch of the 51 mm. mesh showed an increase of 2/5 over 1936, indicative that the young fish just entering the fishery had at least maintained their numbers.

Between 1937 and 1938 no very good direct comparison is possible, but it seems likely there was little change or some decrease in the numbers of the fish caught by small to medium meshes, and some increase in the numbers of the larger fish, owing to absence of nets which would catch them.

TABLE IV. (1) Catch per net-night of squawfish in the spring inshore fishery of 1935, 1936 and 1937; and (2) the number of net-nights used in each calculation.

Mesh	76		70		64		57		51	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
"Shore" nets 1.8 m. deep										
1935	3.1	10	14.2	21	12.7	14	10.9	13	—	—
1936	0.30	84	0.76	72	1.35	134	2.20	61	—	—
Ratio	0.096		0.054		0.106		0.201			
"Shore" nets 1.8 m. deep (76 mm. mesh), and floating nets 2.7 and 3.6 m. deep (smaller meshes)										
1936	0.56	181	1.48	168	1.70	150	3.58	33	0.67	58
1937	0.20	65	0.26	90	0.36	75	1.70	30	0.95	116
Ratio	0.355		0.173		0.212		0.475		1.409	

CHAR

Table V gives the best information available on the change in abundance of char. The early netting, from 1932 to 1934, being all done in relatively deep water, gave the impression that char were much more common than is borne out by catches made since. Even between 1932 and 1934 a marked decline in catch per unit of gear occurred, which is much greater than the moderate increase in gear in use could account for. Between 1935 and 1936 there was a further drop

in catch per unit, in spite of a decrease in gear in use between the years. The catch of large char per unit of gear (meshes 114 to 89 mm.) between 1932 and 1936 was down to approximately $\frac{0.013}{0.83}$ or 1/64 of their original number; for small char (meshes 76 to 64) it was $\frac{0.046}{0.50}$ or 1/11. In terms of actual population numbers, allowance for differences in gear in use might increase these estimates to about 1/20 and 1/4 respectively—or more generally, almost all of the large char were destroyed, and the majority of the smaller ones as well, down to those about 200 mm. in length.

TABLE V. (1) The catch per net-night of char, in July and August, in nets 1.8 m. deep set in deep water, and (2) the number of such net-nights used in the comparison. The first night of any set is rated as two net-nights, the later nights as one only. The number of units of gear indicated is the total used in 1932 and 1934, and very nearly the total that took char in 1935 and 1936.

	1932		1934		1935		1936	
Mesh	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
114	0	(6)	0	(16)	0.084	(203)	0.016	(122)
102	0.83	(6)	0.62	(16)	0.133	(196)	0	(84)
89	1.67	(6)	0.062	(16)	0.189	(196)	0.023	(44)
76	0.67	(6)	0.125	(16)	0.103	(184)	0.023	(44)
70	0.17	(6)	0.44	(16)	0.048	(83)	0.068	(44)
64	0.67	(6)	0.25	(16)	0.042	(48)	0.046	(44)
Averages:								
114 to 89	0.83		0.23		0.14		0.013	
76 to 64	0.50		0.27		0.064		0.046	

After 1936, summer netting for large char was abandoned, though a few were still taken in autumn; since that time they have probably made some small recovery in numbers. Smaller char, presumably the size-classes just entering the fishery, were still being taken in some numbers (table II), but not sufficiently to suggest any marked recovery. The comparison between June inshore catches in 1935 and 1938 (table III) does not include many char, but does suggest a decline rather than an increase over that period.

TROUT

Very few trout were captured prior to 1935. Between that year and 1938 there is a suggestion of some diminution in numbers (table III), the 1938 catch averaging 0.38 of that of 1935. The numbers taken were, however, insufficient to make this a certain conclusion. A comparison, by meshes, between 1935 and 1936 gives little indication of decline in catch per unit of gear except a non-significant one in the case of the 57 mm. mesh. Comparison between spring catches of 1936, 1937 and 1938 (table VI) does not suggest any definite trend in numbers; indeed the results for adjacent meshes are quite varied. The average catch per unit gear of the three meshes 76 to 64 mm., which catch most of the trout, was 0.28 in 1936, 0.24 in 1937, 0.29 in 1938.

TABLE VI. (1) Catch per net-night of trout in April of 1936-37-38, and (2) number of net-nights used in the calculations. (Nets used are 1.8 m. nets set at shore, except (a) in 51 mm. mesh, nets are 3.6 m. deep set floating, and (b) in 76 and 70 mm. meshes, part of the nets were 2.7 m. deep.

	76		70		64		57		51	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
1936	0.149	138	0.431	160	0.246	384	0.151	86	0.100	100
1937	0.580	112	0.089	326	0.038	158				
1938	0.585	181	0.165	103	0.118	178			0.268	242

In general, no satisfactory evidence is available that the netting programme has produced any but evanescent effects upon the trout populations of the lake; certainly no reductions of the magnitude inflicted upon squawfish and char. This is in spite of the fact that anglers assist by catching a considerable number each year—a number difficult to estimate, but several hundred at least. Two explanations may be advanced which could account for this: (1) Trout are to a great extent neither shore nor bottom fish; anglers take them readily by trolling at rather shallow depths off shore or in open water. Hence even the considerable number taken by nets in various years may represent only a small fraction of their total numbers. It seems likely that this is substantially true, for both large and small trout have maintained their numbers. (2) It is possible that young trout have benefitted more in survival rate from predator control operations than have the young of squawfish or char. This may be suggested by an increase in small trout taken at the counting fence in 1938.

COHO

There is considerable evidence that the coho salmon which mature in the lake are largely the progeny of the spawning of anadromous fish. Hence the fluctuations in the numbers of these spawners in recent years, rather than any fisheries which have been prosecuted, have been the primary factor governing the abundance of coho in the lake. The coho caught are readily separable into age groups on the basis of length alone. They first appear in the nets of 38 mm. mesh in June of their second year of life, and by autumn have grown to a size which gills in several larger meshes. Early in the following year they are taken in largest numbers, but for reasons unknown only relatively few spawners are found in the autumn. The catch of coho of recent year-classes is as follows:

Year of spawning	1932-33	1933-34	1934-35	1935-36
Year of life when caught II	10	31	57	266
III	13	183	18	167

The low catches from the 1932-33 and (under II) 1933-34 spawnings are to be credited to a very limited fishery, while a poor spawning in 1934-35 yielded few coho in the nets, in spite of intensive fishing. How great a proportion these figures represent of the total coho populations it is not easy to judge, but their removal is doubtless of immediate value, at least, to the sockeye. As with trout, the coho are also killed by anglers, who are said to have taken an unusually large number in the summer of 1938 (third year fish from the spawning of 1935-36).

Changes in Length

When a fishery declines under increasingly intensive exploitation, it is characteristic that the average size of the individuals should decrease, owing to the larger sizes being caught off. Hence, if any considerable reduction in numbers of fish has been effected at Cultus lake, it should result that (1) the average size of predator populations in later years should be less than in 1935, and (2) the average size of the catch of the individual meshes of nets should show some decrease.

A comparison was made for squawfish caught in June (table VII). For the 57 and 64 mm. meshes, there is evident a significant decrease in mean length between 1935 and 1936, and in the second case a further decrease in 1937, with

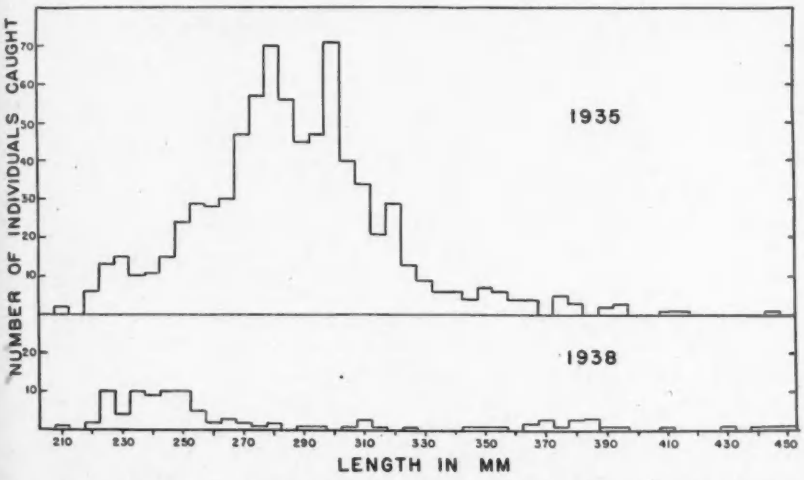

Figure 4. Length frequency distribution of squawfish caught by gill nets, during the "test" periods of 1935 and 1938. The kind and number of nets used was the same in the two years.

only non-significant changes thereafter. The 51 mm. shows a significant decrease between 1936 and 1937, and an *increase* again in 1938. (The latter is probably owing to the fact that during the "test" period of 1938, which occupied most of June, no 51 mm. nets were used, and the smaller fish were not caught off.) The 70 mm. mesh shows no significant change in any year; this can be ascribed to the *relative* increase in large-sized squawfish in the lake, which are caught to some extent in a mesh just below their normal gilling range.

Gill-nets are, however, so selective a type of gear that only limited changes in length of the catch of the individual meshes could occur, which accordingly only show up in large samples. Fortunately, it is possible to compare the total catch of all nets in the "test" periods of 1935 and 1938, when the gear in use was kept uniform between the years. Figure 4 shows very strikingly the near-extermination of the intermediate size range of squawfish, the persistence of the small groups just entering the fishery, and also of the large specimens which have been

TABLE VII. Mean length, standard deviation in length (S), and probable error of the mean length (P.E.), in millimetres, of squawfish taken in June of various years.

	1935	1936	1937	1958
51 mm. mesh				
No. of individuals		145	121	75
Mean		230.8	214.6	220.6
S		12.6	15.8	14.5
P.E.		0.70	0.97	1.13
57 mm. mesh				
No. of individuals	237	293	170	197
Mean	270.9	247.8	244.3	246.7
S	27.3	21.0	20.8	15.4
P.E.	1.19	0.83	1.08	0.74
64 mm. mesh				
No. of individuals	174	504	117	15
Mean	284.3	274.5	264.6	261.3
S	24.8	19.0	24.4	23.4
P.E.	1.27	0.57	1.52	4.07
70 mm. mesh				
No. of individuals	276	309	112	17
Mean	296.4	295.7	299.8	306.5
S	27.4	21.2	38.0	26.5
P.E.	1.11	0.81	2.42	4.33

little fished. The marked reduction in large char is well shown in figure 5. The trout (figure 5) appear also to have declined in their intermediate size range, but the larger ones are probably about as abundant as formerly.

IMPROVEMENT IN SURVIVAL OF SOCKEYE

RESULTS TO 1938

Three different methods of handling the adult spawning sockeye were employed at Cultus lake. By the first method the spawn was taken artificially, held in hatcheries until the fry were hatched and free-swimming, then planted in the lake. The second involved the planting of the eggs when "eyed" in the gravel of streams tributary to the lake. Under the third method the sockeye were allowed to enter the lake and spawn naturally. In the course of the tests of artificial propagation, before predator control was attempted, the efficiency of each of these methods in producing migrant smolts was determined several times (Foerster 1936b, 1938).

Since predator control was commenced, three migrations of smolts occurred, those of 1936, 1937 and 1938, which were the result of eyed-egg planting, natural propagation and fry liberation respectively. The survival obtained each year is shown in table VIII, and compared with the earlier efficiency of these methods.

Considering eyed-egg planting first, the 9.0 per cent tabulated for 1936 is considerably greater than the highest previous figure. The difference in survival between 1936 and the mean of the two earlier years is 5.4 per cent, an increase of

150 per cent; whence an estimate of the number of 1936 smolts saved by predator removal is 300,000.

Comparing, secondly, the survival from natural spawning, it will be seen that the earlier percentages ranged from 1.0 to 3.2, compared with 7.8 obtained since predators have been destroyed. The difference between the last and the mean of the first three is 6.0 per cent, an increase of 340 per cent. The probable number of 1937 smolts which had been saved by the removal of predators is therefore 2,400,000.

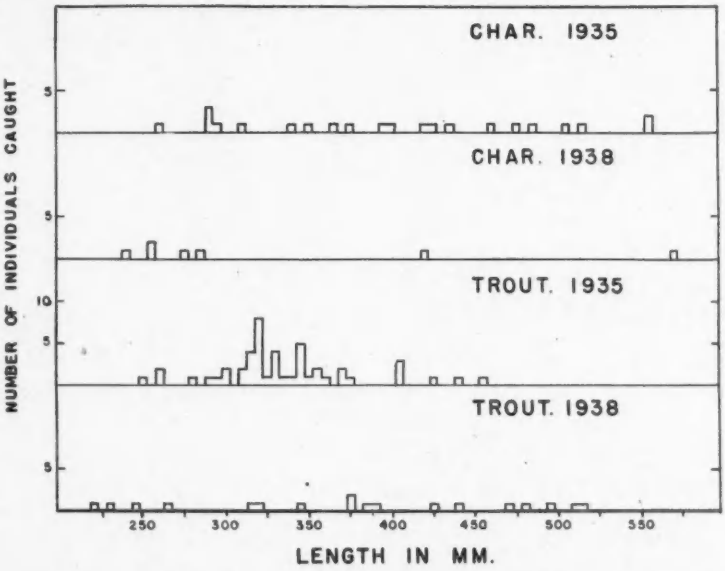

FIGURE 5. Length frequency distribution of char and of trout caught by gill-nets in the "test" periods of 1935 and 1938.

Dealing finally with the survival from the fry liberations, the three determinations made prior to predator control indicate a mean survival rate of 4.2 per cent. The difference between this and the survival obtained in 1938 is 8.9 per cent, an increase of 210 per cent over the earlier figures. The probable number of 1938 smolts which have been saved by removal of predators is therefore 1,100,000.

In testing the significance of the observed increase in survival rate, use is made of the "t" distribution of Fisher (1932), in table IX. The probability (P) in the last column is that the observed average difference between pre- and post-control survival rate could have occurred by chance only. Both natural propagation and fry liberation show an increase in survival after control which is statistically significant (in less than 1 chance in 20 could it have occurred by accident). Considering all three methods together, there is much less than 1 chance in 100 that the improvement could be accidental.

TABLE VIII. Survival of young sockeye salmon to the migrant smolt stage, before and after predator control. The latest year in each case is after predator control had been in progress.

Eyed-egg planting				
Year of migration		1930	1935	1936
Eggs planted		2,650,000	4,372,000	5,590,000
Total smolts		43,400	243,800	501,800
Percentage survival		1.64	5.58	8.98
Natural propagation				
Year of migration	1927	1929	1932	1937
Eggs in females	17,470,000	250,000,000	24,900,000	40,000,000
Total smolts	197,600	2,637,600	788,600	3,125,000
Percentage survival	1.13	1.05	3.16	7.81
Fry liberation				
Year of migration	1928	1931	1934	1938
Fry liberated	5,916,000	9,093,000	4,825,000*	12,468,000
Total smolts	344,500	350,100	135,800*	1,627,000†
Percentage survival	5.83	3.85	2.81	13.05†

*These figures include some non-experimental fish, not a part of the experimental lot described by Foerster (1936b, 1938).

†These figures would be somewhat increased by two-year-old smolts in the 1939 migration.

It may possibly be urged that the differences in survival rate, even though real and significant, are not necessarily to be attributed to the removal of predatory fish, but could be the result of other changes in the lake. Against this possibility may be set the following: (1) every precaution has been taken to see that no artificial disturbance affecting the lake has taken place over the whole period considered; (2) the natural physical conditions in the lake (temperature, etc.) appear to be in no way exceptional (Ricker 1937a, and subsequent MS. data); (3) an apparent improvement in survival rate has been effected with all three methods of propagation (natural, egg planting, fry liberation), showing that the factors of amelioration must act on the fry after they become free-swimming. Hence there are good reasons to suppose they must have been of the nature of a reduction in predation.

One alternative must, however, be considered—that it may be not so much the reduction in predation, as an increase in food available in the environment that has been the beneficial effect of the destruction of fish in the lake. As far as a *direct* effect of this sort is concerned, there is little possibility of any appreciable result. Most of the larger fish caught were of a size that consumes relatively little plankton (trout form a partial exception). The shiners, sticklebacks and squawfish taken in the seines eat plankton to a great extent, but these are in summer largely confined to inshore waters, which sockeye do not frequent. Hence there has been little or no change in the amount of potential sockeye food taken by other species—in fact these various prey species may, like sockeye, now have an increased survival rate. Any *indirect* effect upon basic food conditions in the lake, resulting from the conservation of food materials in whatever form, which

TABLE IX. Significance of the changes in survival rate of young sockeye before and after the beginning of predator control.

	Eyed-egg planting		Natural propagation		Fry liberation		All methods	
	Before control	After control	Before control	After control	Before control	After control	Before control	After control
Percentage survival:								
First test	1.64	8.98	1.13	7.81	5.83	13.05		
Second test	5.58		1.05		3.85			
Third test			3.16		2.81			
Mean	3.61	8.98	1.78	7.81	4.16	13.05	3.13	9.95
Difference	5.37		6.03		8.89		6.82	
Combined variance	7.76		1.43		2.35		4.50	
"t"	1.57		4.36		5.02		4.76	
Degrees of freedom	1		2		2		9	
Probability	0.9		0.05		0.04		less than 0.01	

the destroyed fish would have eaten, would take about a year to become effective, whereas the increased survival rate of the sockeye was effective from the first year of the netting programme. In addition, if the amount of nitrogen or phosphorus in all the fish killed in a year's time be compared with the amount present in other forms in the lake (inorganic salts, etc.) by a method used earlier (Ricker 1937a, p. 398), it will be found that the most liberal allowance will not permit that there be any significant increase in the general supply because of the death of these individuals.

It seems clear therefore that decrease in predation is the only available explanation for the observed increase in survival rate of sockeye.

COMMERCIAL VALUE OF PREDATOR CONTROL

The gains resulting from the control of predators have been computed in terms of increased smolts in migration. To find the commercial value of such increase, the number of resulting adults must be ascertained. Foerster (1936a) has shown that about 9.9 per cent of migrant smolts from Cultus lake return from the sea, to be caught on the fishing grounds or to escape to the lake. Of these, one-half to three-quarters are caught by fishermen. The value of the increase from the three years of control work to date, at current prices, can be approximately calculated as in table X.

The expense involved in predator control work at Cultus lake, from its start in 1935 to the end of April, 1938, was approximately as follows:

	Labour* (2 men)	Nets	Miscellaneous	Total
1935 (7 months).....	$1,645	$400	$ 50	$2,145
1936 (12 months).....	2,820	400	100	3,320
1937 (12 months).....	2,820	400	100	3,320
1938 (4 months).....	940	—	50	970
				$9,755

*The two men were not continuously employed at control work, but in rush seasons some extra help was employed.

The above represents the whole of the control operations which might have affected the seaward migrations of 1936, 1937 and 1938. The migrants saved in these three years, over and above normal survival prior to 1936, were estimated

TABLE X. Value of the increased migrations of sockeye following predator control. Extra adults (column 4) are calculated as 10 per cent of migrants, and of these the minimal fraction of one-half is credited to the fishery (column 5). Their average value when caught is estimated as 50 cents each (column 6); and the value of the canned product (column 7) is calculated as $14.00 a case, with 14 fish to a case. (Fraser sockeye average about 12 to a case, but the Cultus fish are smaller than most of the river's runs).

Year of migration (1)	No. of extra migrants (2)	Year of catch (3)	No. of extra adults (4)	Minimal increase in catch (5)	Value to fishermen (6)	Value when processed (7)
1936	300,000	1938	30,000	15,000	$ 7,500	$ 15,000
1937	2,400,000	1939	240,000	120,000	60,000	120,000
1938	1,100,000	1940	110,000	55,000	27,500	55,000
	3,800,000	....	380,000	190,000	$95,000	$190,000

above as 3,800,000 in all. The cost of control operations therefore is 0.26 cents per migrant immediately saved.

However, the operations to date will have considerable effect in improving survival for some years into the future, for two reasons. Even were control measures to be stopped, the predators would probably need two or more years to recover their former abundance and re-establish the former rate of predation; while the effects of the increase in salmon breeding stock upon future runs may extend for a much longer period. To estimate the magnitude of these future benefits is not easy, but they must be reckoned at least as great as those obtained to date. On this basis, the cost of control operations, per yearling saved (past and future) would be reduced to 0.13, or approximately 1/8 of a cent.

Given the 10 per cent survival rate to the adult stage, the cost of control work has been therefore of the order of 1.3 cents per adult salmon added to the run.

FUTURE BALANCE BETWEEN SOCKEYE AND PREDATORS

From table IX, the average increase in survival rate since predator control has been started is from 3.13 to 9.95 per cent. In other words, where one sockeye survived formerly, more than three now live to go to sea. Observations to date give no hint that the new survival rate could not be maintained at even higher levels of sockeye population than have been under observation so far. Even before predator control operations, the sockeye running to the lake showed no general tendency to decrease in numbers (cf. the adult migrations, Foerster 1938), though of course when large numbers of eggs were transferred to other areas a temporary decrease followed. It appears therefore that if the new conditions of lacustrine survival are maintained, and no increase in mortality during the migratory and marine life of the fish occurs, the lake's run of sockeye should rapidly increase—at least tripling itself every four years. Obviously such a process cannot continue indefinitely; new factors must sooner or later appear which would keep their numbers in check. Possible new checks may be either natural or

artificial. Either kind, if it is to maintain population balance, must exert a greater proportionate effect as numbers increase (Nicholson 1933). A discussion of examples will illustrate different aspects of the problem of maintaining optimum population numbers.

(1) Fundamental to all discussion of the effects of increased population numbers is the ascertained fact (Foerster MS., quoted in Ricker 1937b, p. 466) that the size of the year-old migrants issuing from the lake, prior to predator control, was inversely correlated with their abundance. The coefficient of correlation between number and average weight, from 1927 to 1935, was calculated as -0.806, which is significant to a probability of 0.01. Chief contribution to the correlation was made by two years of very numerous and very small migrants —the smallest being of the migration of 2½ million in 1929.

This phenomenon is suggestive of a limited food supply in the lake, a suggestion which is reinforced by an inverse correlation between available plankton food and sockeye populations, over several years (Ricker 1937b). Possible effects of a "space-factor", independent of food available, in reducing growth rate, may perhaps also be considered.

Small migrants may conceivably be somewhat less well equipped to survive their migrations and ocean life than are larger ones, though any such effect is not noticeable in their percentage return as adults (Foerster 1938). More important probably are the indirect effects of small size, discussed below.

(2) An obvious natural check on abundance would be a greater natural mortality among fingerlings of large populations, from the increased attack of parasites and diseases, owing to crowding and/or malnutrition. Very little is known concerning such enemies of Cultus lake sockeye, but there is an external copepod parasite and various internal parasites which might assume importance, if other controlling agents failed to keep the population within bounds.

(3) A more subtle effect of decreased average yearling size might be a reduction in the proportion which actually go down to sea at the end of their first year. It is known (Foerster 1929) that two-year-old migrants consist of fish which had made, during their first year, much less than the average growth of year-old migrants. From this devolves the possibility that under conditions of poor growth a really large proportion of the migrants might stay in the lake an extra year. The effect of this in reducing migrant production would consist in (a) additional mortality suffered by these fish during their second year of lake residence, and (b) their indirect effect upon growth and survival of the fingerlings of the next year-class, which would have to meet the competition of these older fish.

The situation is further complicated by the existence of non-migratory "residual" sockeye derived from anadromous parents (Ricker 1938). These appear most numerously among sockeye which have had slow fingerling growth followed by rapid yearling growth—as happens when the "left-overs" from a large population live with a small population the next year. Growing to as much as four years of age in the lake, these fish individually consume large quantities of plankton suitable for fingerlings, and in addition are predatory upon newly-emerged fry.

Both the residual and two-year-lake habits are evidently unfavourable for a maximum production of migrant smolts. It is in fact not hard to see the possibility that a moderately large number of fry might not only have a greater survival rate than an extremely large number, but might even produce a greater absolute number of migrants.

(4) Increased lacustrine predation upon sockeye is still a possible limiting factor for the future population balance. That is, it is conceivable that some predaceous species, after an initial set-back from the netting operations (or perhaps without it, in the case of trout) may be able to exist and increase in some part of the habitat that the nets do not greatly affect. In addition, because the sockeye of very large populations would be of smaller size, and also simply because they would be more numerous and more easily found, more might be taken in the future, per individual predator, than at present.

The association between large migrations and small size of migrants, *prior to predator control*, was mentioned above. Since control was begun, however, two large migrations have occurred, one of them the largest on record—3,100,000 fish, in 1937. In neither cases is any dwarfing noticeable, the migrants being of a large average size. The reason appears obvious: with the greater survival rate now prevailing, it takes only about a third as many newly-hatched fry to produce a given number of migrants, with the result that competition for food in summer (the principal growing season) is now much less acute than in former years, comparing migrations of the same size.

It can be claimed therefore as a further very important advantage of the destruction of predaceous fish, that it will permit a much greater maximum population of sockeye to inhabit the lake than has been the case heretofore. What this maximum population will be cannot be estimated with any exactness, but from the reasoning above it follows that it should be *at least* such as to produce three times the 1929 smolt migration, or 7,500,000 migrants.

If the suggestion above is valid, that the lake's productive capacity is limited by the size of the *summer* sockeye population it can maintain, then a desirable predator to maintain smolt production near its maximum value would be one which bears heavily on eggs, fry and early-summer fingerlings, and little or not at all on autumn and winter fingerlings, or yearlings near time of migration. Of the four important species earlier referred to, it is evident that the squawfish would be least desirable, in that it takes practically no very young fry, and eats most heartily of the migrants of March and April. The three other species are none of them ideal predators, considered from this point of view, but the trout appears to be the best available, as it consumes rather more individuals in May to July, in relation to its consumption from (say) October to April, than do coho or char.

The considerations of the last paragraph must, of course, be applied only to the anticipated future condition of near-maximum sockeye populations. For the present, when the purpose is to increase populations as rapidly as possible, there is little to choose between the various species of predators.

(5) Extension of the argument of the last section indicates that, in the future, man himself will be an ideal "predator", in that he can directly regulate

the number of fry produced, by limiting the number of spawners that enter the lake. This procedure would have an added value in the opportunity it presents for an attempt at selective breeding for desirable commercial qualities such as larger size and earlier seasonal return from the sea. Another advantage would be its selectivity: the four cycle years of sockeye are not likely to attain optimal numbers simultaneously, hence a method of regulation adjusted to each individually is desirable. In addition, there has been in the past no difficulty in disposing of fish slaughtered at the lake to individuals for human consumption, so this method would increase the food values obtained from the run.

(6) A question arises, then, of whether or not the lake's maximal production of migrants would really be obtained by admitting adults of all four cycles in equal numbers. It is well known that the Fraser river sockeye exhibited from the earliest times the phenomenon of a "dominant" cycle year, whose numbers exceeded by many times those of the other three cycles. The same phenomenon is today a strongly-marked characteristic of individual runs to various areas. No satisfactory evidence of the cause of this condition has yet been advanced, though it is not difficult to construct plausible hypotheses. Two which deserve consideration, singly or in combination, are as follows: (a) that the abundance of predators in a lake limits and is limited by the size of the smallest sockeye run of the four, plus what outside food they can obtain, so that any cycle which very greatly exceeds this minimum suffers less, proportionately, from predation, and must increase until some other factor limits its numbers; (b) a very large population of sockeye would, from analogy with findings at Cultus lake, have a relatively high proportion of two-year-old migrants and residual non-migrants, both of which would act unfavourably upon the survival rate of the cycle years following.

Whatever the cause, cyclic variation appears to be a fundamental characteristic of many natural populations, although not therefore *necessarily* a desirable feature of populations artificially regulated. Whether best production from the lake can be obtained with equal, or unequal, cycle numbers, must be made a matter for future experiment.

Relation of Sockeye to Game Fish

Although emphasis has been placed upon the reduction in predation effected by netting the lake, the reader should not lose sight of the fact that there is still a very large number of young salmon killed in the lake each year. The percentage survival of fry planted was 13 per cent in 1938—a figure which, though considerably greater than in early years, still leaves 87 per cent of the young sockeye destroyed between free-swimming fry and migrant stages. Doubtless causes other than predation are responsible for some of this mortality, yet it is clear that an ample number of sockeye still remains available to what predators are able to escape destruction. Not only this, but the ultimate effect of predator control will be to increase, by several to many times, the absolute number of sockeye so consumed, as their populations increase in size in years to come.

If, in these coming years, the predators remaining in the lake consist largely of the useful salmonids, especially the trout, then the benefits of predator control will be extended into a field where they are little anticipated, at least by the sport fishermen concerned. As was shown earlier, it is in fact the useless squawfish which has suffered severely from the netting done to date, while the valuable trout has declined relatively little, if at all. If this is the present situation, then it must be anticipated that in the immediate future the trout will enjoy a period of more abundant food, quicker growth, and possibly greater rate of survival.

That the differential attack of the gill-nets should have occurred in precisely the manner it has, could scarcely have been predicted in advance. As shown in the last section, it is not only the anglers' good fortune that the trout have been least attacked. The presence of a population of trout, rather than squawfish, as principal predators in years to come, is to be favoured not less because of their sporting value, than by reason of their more favourable seasonal attack on the young sockeye.

Applicability to Other Lakes

The control of predatory fish at Cultus lake has been both successful and inexpensive, as measured in terms of immediate increase in the commercial catch. In considering its extension to other sockeye waters, several considerations enter. Almost all British Columbia sockeye lakes are larger than Cultus lake, some of them many times larger. Hence the physical work of killing the fish would tend to be much greater. Offsetting this to some extent is the probability that many lakes will offer better opportunities for control work. For example, some have beaches where seines could be used large enough to take adult squawfish in numbers—a procedure impossible at Cultus. Others may offer better opportunities to take fish during a migration period, in streams entering or leaving the lake. There is, of course, little doubt that to effect a significant decrease in the predators of large lakes such as Shuswap or Quesnel would be a more expensive task than has been the case at Cultus. Its net cost, per fingerling saved, would depend on the size of the run to be benefited. If this were small, the cost per fish would be correspondingly great. However, distinction must be made between the immediate and the ultimate benefits of the work. Significant increases in fingerling survival rate should also increase the numbers of adult spawners, and this in turn produce a cumulative increase in the population every four years. Hence the benefits from one year's improvement in survival will extend many years into the future, and this must be considered in assessing the value of control measures. Considering that most sockeye lakes now have very poor runs compared to former years, this is in fact the principal value which increased survival would have, and would justify considerable expenditures. At the moment the important problem is to restore the runs to these lakes to something near their former abundance. When this is accomplished, it will be time enough to determine whether or not the maintenance of populations in excess of those numbers, by means of continued control work, would be economically desirable.

The kinds of predators in other lakes of course differ somewhat from Cultus. For example, ling (*Lota maculosa*) and lake trout (*Cristivomer namaycush*) are found in many lakes of the interior, while squawfish are said to be absent from some. In the end, it will remain a matter of experiment to find to what degree the predators in any given lake are susceptible to economically feasible control measures. A possible means of reducing the cost of such would be to sell part of the catch on the market. Indeed, as non-subsidized commercial fisheries exist, or have recently existed, on some large British Columbia lakes, the greater part of the financial burden might perhaps be met in this manner.

The success of predator control work at Cultus lake does not guarantee its practicability elsewhere, but it does provide a promising new approach to the problem of restoring our sockeye fisheries.

SUMMARY AND RECOMMENDATIONS

Gill-nets have been used on Cultus lake to kill as many as possible of the fish which prey upon young sockeye salmon. Of the four principal predaceous species, 10,130 squawfish, 2,300 trout, 760 char, and 720 coho salmon were killed from May, 1935 to June, 1938.

From the decline in catch per unit of gear set out, it is apparent that squawfish more than 200 millimetres long have been decreased to about 1/10 of their original abundance, and char to about the same extent. Trout may have decreased somewhat but that is not certainly established; in any case they were very much less affected than squawfish or char. Coho show considerable variation in numbers due to variable spawning escapements, which obscures any effect the netting may have had.

Concurrently with the destruction of predators, the survival rate of the young sockeye salmon which live in the lake showed a marked increase, as measured by the number of migrant smolts counted each spring. The survival rate of eyed-egg increased to 8.98 per cent from a previous average of 3.61 per cent; the survival rate of free-swimming fry planted in the lake increased to 13.05 per cent from a previous average of 4.16 per cent; the survival rate of eggs in female sockeye spawning naturally increased to 7.81 per cent from a previous average of 1.78 per cent.

The direct effect of reduced predation, rather than indirect changes in food or other factors, appears to be responsible for most or all of this increase in rate of survival.

Because of the smaller number of fry now needed to produce each migrant, the drain upon the lake's food supply in summer is relieved, and the maximum number of migrants which the lake can produce each year appears to be greatly increased.

Though done solely on an experimental basis, the predator control operations are estimated to have saved and added to the seaward migrations 3,800,000 smolts, up to 1938. These are expected to yield 380,000 adults, of which the fishermen's minimum catch would be valued at about $95,000.00 in the round. The cost of the control operations has been less than $10,000.00, or about 2½

cents per surviving adult. Cumulative future benefits from the work of 1935-1938 will increase the total yield to fishermen, and considerably decrease its cost per fish saved.

It is recommended that control of predaceous fish be continued on Cultus lake, in order that survival rates may be studied among sockeye populations larger than any so far observed. Alternatively, it could be continued simply as a procedure of proven commercial value.

It is recommended that similar experiments be tried on other lakes, in order to determine the value of control operations under different environmental conditions. The outstanding success at Cultus lake makes it appear probable that there will be other lakes where application of similar methods will build up sockeye populations rather quickly from present low levels of abundance.

ACKNOWLEDGEMENTS

The experiment in controlling predaceous fish at Cultus lake was a part of the sockeye salmon investigations of the Fisheries Research Board of Canada, continued through the spring of 1938 by the International Pacific Salmon Fisheries Commission. We have great pleasure in acknowledging the help of Dr. W. A. Clemens, then Director of the Board's Pacific Biological Station, in planning and carrying out the work from its beginning. Other members of the staff of the Station have lent their advice and criticisms, and, in the case of Dr. A. L. Pritchard, considerable aid in the actual field work. Mr. W. F. Baxter was largely in charge of the actual fishing operations, ably assisted by Messrs. G. G. Thompson and E. L. Kennedy. To their conscientious labour and perseverance is due the success of the netting campaign.

REFERENCES

FISHER, R. A. Statistical methods for research workers. Oliver & Boyd, Edinburgh, 4th ed., 1932.

FOERSTER, R. E. *Contr. Canad. Biol. Fish.* N.S. **5** (3), 57-82, 1929.
J. Biol. Bd. Can., **3** (1), 26-42, 1936a.
Bull. Biol. Bd. Can., **53**, 1-16, 1936b.
J. Fish. Res. Bd. Can., **4** (3), 151-161, 1938.

FOERSTER, R. E., AND W. E. RICKER. *Verh. Int. Verein. Limnologie*, **8** (3), 151-167, 1938.

NICHOLSON, A. J. *J. Animal Ecol.*, **2** (1), 132-178, 1933.

RICKER, W. E. *J. Biol. Bd. Can.*, **3** (4), 363-402, 1937a.
Ibid., **3** (5), 450-468, 1937b.
J. Fish. Res. Bd. Can. **4** (3), 192-218, 1938.
Ibid, **5** (3), 293-313, 1941.

Growth of the Rocky Mountain Whitefish

By J. L. McHugh
Pacific Biological Station

(*Received for publication February 3, 1941*)

ABSTRACT

The scale method of age determination has been used to study rates of growth of the Rocky Mountain whitefish, ***Prosopium williamsoni*** (Girard), which vary considerably in different localities, and can be correlated to some extent with altitude or temperature. A curve is given showing the relationship between growth of scale and body. Fast-growing individuals tend to maintain their superiority in growth rate throughout their existence. Slow-growing races live longer and eventually reach a maximum length similar to that of fast-growing fish.

INTRODUCTION

The Rocky mountain whitefish, *Prosopium williamsoni*, is limited in its distribution to the rivers and lakes of southwestern Canada and the northwestern United States. Specimens have been taken in the headwaters of the Athabaska, Skeena, Saskatchewan, and Columbia river systems, and from several sections of the Fraser river. In the U.S. northwest the species is found in the Columbia and in the headwaters of the Missouri river, as well as in many of the smaller streams.

In a previous paper (McHugh 1939) the author has presented data on the age and growth of *Prosopium williamsoni* in Okanagan lake. So far as is known, the literature contains no other detailed report on the growth of this species.

MATERIAL AND METHODS

Scales were examined from a total of 712 individuals, including specimens collected by Dr. D. S. Rawson in National parks in the Rocky mountain region of Canada, by Drs. R. E. Foerster and W. E. Ricker in Cultus lake, and by Mr. Wm. Stevenson in the Elk river. In addition, collections of *Prosopium williamsoni* from the U.S. National Museum and the University of Michigan Museum of Zoology were made available for examination.

Scales were taken when possible from the left side of the fish, in the area between the lateral line and the base of the dorsal fin. Standard length was used to indicate size, being the distance from tip of snout to end of vertebral column.

J. Fish. Res. Bd. Can. **5** (4), 1941

Printed in Canada

ACKNOWLEDGMENTS

The author is indebted to Dr. D. S. Rawson for the opportunity to examine the material collected by him in the National parks of Canada in the Rocky mountain region, and for permission to make use of the resulting data; to Drs. R. E. Foerster and W. E. Ricker for permission to examine their collections from Cultus lake; to Mr. Wm. Stevenson, who provided a sample from the headwaters of the Columbia river; and to Dr. Leonard P. Schultz of the U.S. National Museum and Dr. Carl L. Hubbs of the University of Michigan, for the loan of the collections of *Prosopium williamsoni* from their respective institutions.

The work was carried out in part at the University of British Columbia and in part at the Pacific Biological Station. The facilities provided by both institutions were greatly appreciated, and it is a pleasure to acknowledge the advice and criticism of Dr. C. McLean Fraser and Dr. W. A. Clemens.

RESULTS

Sufficient work has been done on the various species of coregonid fishes to establish the validity of the scale method of age determination when applied to members of this group. Each annulus was considered as representing the completion of a year's growth. In general, it was found that slow-growing fish from the cold mountain lakes possessed scales which were relatively easy to read, due to the clearness of the growth checks and the absence of confusing "false" checks. On the other hand, the annuli on scales of the faster-growing races tended to be much less distinct and hence the age more difficult to determine. This corresponds with an increase in the clarity of the markings on scales of the Pacific herring (*Clupea pallasii*) from south to north (Tester 1937).

Growth Rate of the Sexes

In the coregonid fishes generally, a sexual difference in growth by weight may be demonstrated, but no significant difference occurs in rate of growth in length. As found by Van Oosten (1929) for lake herring (*Leucichthys artedi*), and by Hart (1931) for whitefish (*Coregonus clupeaformis*), no difference between the sexes is seen in growth curves for fast-growing, slow-growing, or intermediate populations of *Prosopium williamsoni* (figure 1).

Local Variation in Rate of Growth

Considerable variation in growth rate for different localities is shown by the data in table I as well as by those plotted in figure 1. The fish from Bow lake show the slow growth of a cold mountain lake, and those from Cultus lake the relatively rapid growth characteristic of warmer waters and lower altitudes. The growth shown for all localities from which samples were examined varies considerably between the two extremes. The figures in table I represent average length at time of capture. Since most of the samples were collected in the summer months, these figures may be considered as comparable, but it must be remembered that the values represent the approximate length attained by midsummer, rather than at the end of the year's growth.

TABLE I. Average standard length of Rocky mountain whitefish at time of capture for each age group

Locality	Average length in millimetres at time of capture for each age group																
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Bow lake	43	77	104	117	160	142	158	186	197	220	...	275	320	...	...	...	375	
Lake Louise	34	66	145	160	180	...	190	...	198	...	...	...	...	...	...	...	...	...
Hector lake	37	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Lake McDonald	52	113	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Bowman lake	85	110	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Logging lake	..	116	156	181	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Emerald lake	..	...	...	190	210	235	250	...	302	...	...	...	...	...	...	...	...	...
Green river	..	...	165	179	196	219	...	...	...	...	...	...	...	...	...	...	...	...
Fremont lake	..	...	...	...	248	...	...	...	...	...	...	...	...	...	...	...	...	...
Snake river	..	...	208	237	234	...	...	...	...	...	...	...	...	...	...	...	...	...
Elk river	..	126	179	203	231	...	...	...	...	...	...	...	...	...	...	...	...	...
Bow river:																		
near lake Louise	..	...	...	...	...	217	...	...	...	...	...	...	...	...	...	...	...	...
Lac des Arcs	..	133	171	...	...	245	...	285	...	320	...	...	...	...	...	...	...	...
near Exshaw	48	145	185	...	227	...	...	290	...	...	...	...	...	...	...	...	...	...
Kananaskis reservoir	..	...	171	211	...	267	245	285	294	...	...	...	...	...	...	...	...	...
Waterton lake	75	131	171	217	225	260	...	290	...	355	...	...	330	...	390	...	...	...
Lake Minnewanka	..	...	171	237	256	273	307	340	375	...	...	...	...	...	...	...	...	...
Third lake	..	...	...	222	245	...	...	332	355	...	...	...	...	...	...	...	...	...
Fraser river (Golden)	81	128	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ghost river reservoir	..	146	199	241	284	...	...	332	355	...	...	...	...	...	...	...	...	...
Hoback river	41	...	230	256	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Big Lost river	78	158	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Blitzen river	59	155	214	240	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Cultus lake	..	112	218	261	254	305	340	353	366	...	...	...	...	...	...	...	...	...

In general, these variations in growth rate may be correlated with the peculiar physical characteristics of the bodies of water in which the fish originated. Bow lake and lake Louise, at the headwaters of the Bow river in southwestern Alberta, are glacial lakes at altitudes of 6,500 and 5,680 feet (1980 and 1730 m.) respectively, and in addition to being cold, their waters are heavily silted. This combination of low temperature and low light intensity apparently results in slow-growing whitefish populations. Hubbs and Cooper (1935) have correlated growth variations in *Xenotis megalotis* and *Apomotis cyanellus* with temperature and with the number of days in the growing season. The sample from Hector lake consisted entirely of fish in their first year, but their small size in late summer and the similarity in altitude between this and the previous two lakes suggests a similar rate of growth.

Cultus lake and its outlet stream in southwestern British Columbia are situated close to the coast and drain into the Fraser river system at an altitude of less than one hundred feet (30 m.) above sea level. The water is comparatively warm, particularly in the summer season, and the rate of growth is correspondingly high. Similar growth rates are encountered in (1) the Ghost river reservoir, draining into the Bow river in Alberta, which, although at a fairly high altitude (approximately 4,000 feet or 1,200 metres) supports a fast-growing population; (2) the Hoback river, Wyoming, and the Big Lost river, Idaho, both of which drain into the Columbia; and (3) a diversion ditch off the Blitzen river in Oregon.

In the Columbia river system the whitefish found in the upper reaches grow rather slowly. This is characteristic of lake McDonald, Bowman and Logging lakes in northwestern Montana, which lie at an elevation of approximately 4,100 feet (1,250 m.) and drain into the Flathead river, and also of Emerald lake in southeastern British Columbia, which is 4,272 feet (1,300 m.) above sea level and drains into the Kicking Horse river. At lower altitudes in the Columbia growth is faster, as illustrated by the data for Fremont lake and

the Snake river in Wyoming, and the Elk river at an elevation of 3,800 feet (1,150 m.) in southeastern British Columbia.

In the Saskatchewan river system a similar increase in size with decreasing altitude may be seen. In the Bow river, for example, specimens in their sixth year taken at 5,000 feet (1,500 m.) near lake Louise are smaller than those from the vicinity of Lac des Arcs or Exshaw which are roughly 4,200 feet (1,300 m.) above sea level. Fish from Kananaskis reservoir and from Waterton lake, both of which lie at approximately the same altitude as Lac des Arcs, are similar in rate of growth. Third lake and lake Minnewanka, although at elevations of 4,500 and 4,770 feet (1,370 and 1,450 m.) respectively, are relatively warm and support rather fast-growing populations.

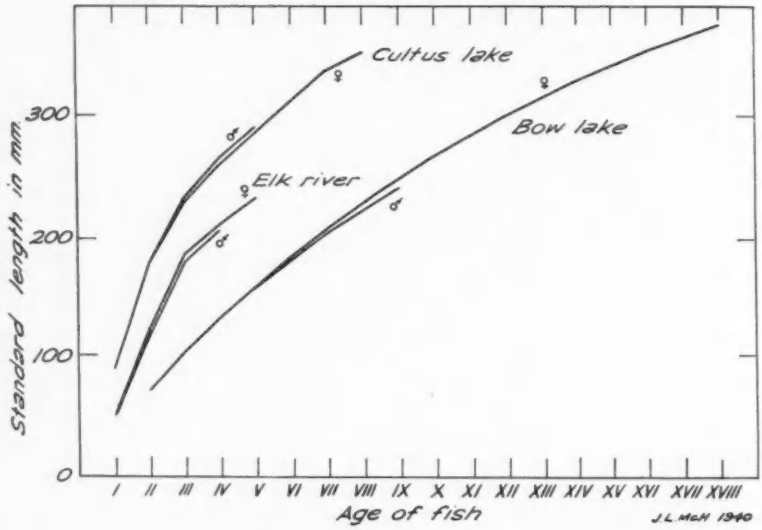

FIGURE 1. Growth curves for both sexes in populations having fast, intermediate, and slow rates of growth.

A sample from the Green river, Wyoming, which is a tributary of the Colorado river system, was found to be relatively slow in growth.

In a previous paper (McHugh 1940) it was shown that the type of food taken differed considerably in some localities. A comparison of the food and growth data shows that in some cases variations in diet are accompanied by differences in growth rate.

DIFFERENTIAL GROWTH OF SCALE AND BODY

To obtain a reliable average for the length at the end of each year of life it is sometimes desirable to make use of the lengths as calculated from the growth increments of the scales. If it is assumed that scale and body increase

in length in a constant ratio, "Lee's phenomenon" appears, the calculated lengths for the early years of life becoming progressively smaller as the fish from the scales of which they are calculated increase in length (Lee 1912, Creaser 1926, Van Oosten 1929, Hile 1936). It has been recognized for some time that the ratio of scale length to body length does not remain constant as the individual increases in size, and from the material available it appears that this offers a reasonable explanation for the occurrence of "Lee's phenomenon" in *Prosopium williamsoni*. For each individual an average value was obtained for the length of the anterior radius by measuring several scales from the region between the lateral line and the insertion of the dorsal fin. In fish of various lengths from a number of localities it was found that the ratio remained relatively constant for individuals of the same *size* irrespective of age or locality, and

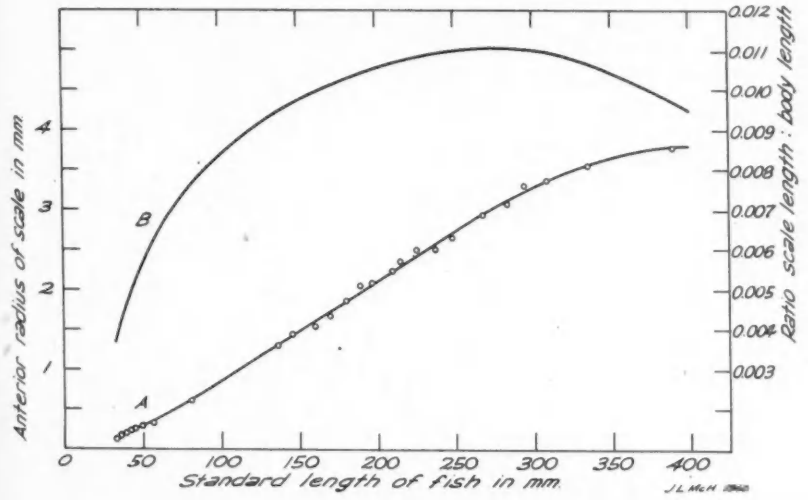

FIGURE 2. Relation between standard length of fish and: A,—anterior radius of scale; B,—ratio of scale radius to fish length.

therefore the data were combined to produce a curve which would apply to all the populations of *Prosopium williamsoni* studied. This curve (A in figure 2) is similar to that obtained by Creaser (1926) for *Eupomotis gibbosus*. When the ratio of the anterior radius of the scale to the standard length of the fish is calculated from this curve and plotted against standard length, curve B results. This second curve indicates that the scale increases in length relatively more rapidly than the fish until a standard length of approximately 250 millimetres is reached. Past this point the relative growth rate of the body overtakes and eventually may exceed that of the scale.

A reasonably accurate approximation to the true average lengths at the end of each year of life for any particular year class may be obtained from the average scale measurements as follows: From curve A read the scale length

corresponding to the average length of the fish at the time of capture. Take the distances measured along the anterior radius to each winter check and divide the scale length obtained from the curve in the same proportions. Use the values so obtained to read the lengths of the fish from the curve.

The reliability of the data on which these curves are based depends on the extent of selectivity due to such causes as differential addition and subtraction of individuals in the population and selection by the fishing gear employed. In the present case such factors cannot be measured, but since the application of the method appears to produce a reasonably satisfactory result, it must be assumed that errors of this sort are small in comparison with that introduced by the differential growth of scale and body.

Growth Compensation

Hubbs and Cooper (1935) have shown for *Xenotis megalotis peltastes* that those individuals which grow slowly in their early life continue to do so throughout their existence, and thus increase their variability in size with age. In other species the reverse is the case, and those fish which at first grow slowly tend to increase their rate of growth in later years, hence becoming more uniform in size with increasing age. This has been termed "growth compensation", and is described by Hile (1936) for the cisco (*Leucichthys artedi*). Foerster (1936) found for young sockeye salmon (*Oncorhynchus nerka*) that although growth compensation might occur in fish of one year class, it did not necessarily take place in succeeding years.

Apparently growth compensation does not take place in any of the populations of *Prosopium williamsoni* studied. The coefficient of correlation between growth of successive years was calculated for several samples (table II). In some cases, for example Cultus lake and lake Minnewanka, little or no significant correlation exists between the growth of the first two years, but during subsequent periods of growth the relation between the length becomes more and more exact. All such correlations are definitely positive, not negative as would be the case in growth compensation.

Table II. Correlation between growth of successive years in the Rocky mountain whitefish

Locality	Coefficient of correlation (r)			
	1st–2nd year	2nd–3rd year	3rd–4th year	4th–5th year
Elk river	+0.74; $P<0.01$	+0.65; $P<0.01$		
Bow lake	+0.65; $P<0.01$	+0.86; $P<0.01$		
Cultus lake	+0.23; $P<0.02$	+0.74; $P<0.01$	+0.95; $P<0.01$	
Lake Minnewanka	+0.43; $P<0.03$	+0.89; $P<0.01$	+0.94; $P<0.01$	+0.95; $P<0.01$

Compensation of a different type, however, is illustrated in figure 1 and table I. Apparently the slow-growing races, although smaller at any given age, live longer and eventually reach a size comparable to that attained by the

faster-growing populations. In Bow lake, for example, specimens have been taken at ages up to seventeen or eighteen years, while in Cultus lake the oldest fish taken were in their ninth year.

SUMMARY

A study of the growth rate of Rocky mountain whitefish from various localities in southwestern Canada and in the northwestern United States shows that considerable variation occurs. This is apparently associated with climatic factors, the species being smaller for any given age with increasing altitude. No distinction can be made between the sexes in growth by length. In comparing the growth of scale and body it is evident that the scale grows more rapidly in length up to a certain size, during which time the body increases its relative rate of growth until it eventually exceeds that of the scale. Individuals which grow slowly during early life do so throughout their existence, and therefore the variability in size tends to increase with age. Slow-growing races tend to live longer, and eventually reach a maximum size equal to that of populations having a higher growth rate.

REFERENCES

CREASER, C. W. *Univ. Mich. Misc. Pub. Mus. Zool.*, **17**, 1-82, 1926.
FOERSTER, R. E. *J. Biol. Bd. Can.*, **2** (3), 311-333, 1936.
HART, J. L. *Contr. Canad. Biol. Fish.*, **6** (20), 429-444, 1931.
HILE, R. *Bull. U.S. Bur. Fish.*, **48** (19), 211-317, 1936.
HUBBS, C. L., AND G. P. COOPER. *Pap. Mich. Acad. Sci. Arts Lett.*, **20**, 669-696, 1935.
LEE, R. M. *Pub. Circonstance*, **63**, 1-34, 1912.
MCHUGH J. L. *Bull. Fish. Res. Bd. Can.*, **56**, 39-50, 1939.
J. Fish. Res. Bd. Can., **5** (2), 131-137, 1940.
TESTER, A. L. *J. Biol. Bd. Can.*, **3** (2), 145-168, 1937.
VAN OOSTEN, J. *Bull. U.S. Bur. Fish.*, **44** (1053), 265-428, 1929.

The Nutritive Value of Marine Products. XV.

Proximate Analyses of Canned British Columbia Crabs, Shrimps and Clams

By L. I. Pugsley

Laboratory of Hygiene,
Department of Pensions and National Health

(*Received for publication April 21, 1941*)

ABSTRACT

Percentages of moisture, protein, fat and ash in meat and liquor were determined. Food value of the meat was approximately 100 calories per 100 grams.

The nutritive value, expressed as the percentage of protein, carbohydrate and fat of foodstuffs is of importance in calculating the calorific value of diets and for the evaluation of foods. Carter (1936), Riddell (1936) and White (1936) have determined the nutritive value of a number of canned British Columbia fish, and Tully (1936) has reported the analyses of oysters. In order to contribute further to this series on the nutritive value of the canned fisheries products of British Columbia, the proximate analyses of canned crabs, shrimps and clams were undertaken and carried out when the author was on the staff of the Pacific Fisheries Experimental Station.

METHODS

The canned crabs (*Cancer magister*), shrimps (presumably *Pandalus borealis*) and clams (*Saxidomus giganteus*) were obtained from a local cannery at Prince Rupert, B.C. The analyses were carried out on four cans selected at random from cases of forty-eight cans. The analyses of the soft-shelled clams (*Mya arenaria*) were made on a lot of fifty clams obtained from Masset, Queen Charlotte islands. Thus far this clam has not been utilized extensively for commercial canning.

The total contents of the cans were weighed, the free liquor decanted off and the meat and liquor weighed separately. The meat was ground in a food chopper, thoroughly mixed and aliquots of the minced meat and decanted liquor were analysed separately. Moisture was determined by drying in a vacuum oven at 75°C. until constant weight was obtained, protein by the macro Kjeldahl method using the factor 6.25 to convert nitrogen to protein, fat by extraction with petroleum ether using a Soxhlet extractor and ash by ignition in a muffle furnace at 450°C. to constant weight. The carbohydrate content of the clams was calculated by difference and the calorific value calculated on the basis that 1 gram protein yields 4.1 calories, 1 gram carbohydrate 4.1 calories and 1 gram of fat 9.3 calories.

J. Fish. Res. Bd. Can. 5 (4) 1941

Printed in Canada

RESULTS

From the data on the distribution of meat and liquor (table I), it is seen that

TABLE I. The distribution of the meat and liquor in canned crabs, shrimps and clams

Sample	Total contents (grams)	Meat (grams)	Liquor (grams)
Crabs			
Range	187–207	151–161	27–46
Mean	195	158 (81.0%)	37 (19.0%)
Shrimps			
Range	292–308	124–128	173–180
Mean	303	126 (41.6%)	177 (58.4%)
Clams			
Range	398–440	143–149	255–291
Mean	418	145 (34.7%)	273 (65.3%)

the canned crabs yield the highest percentage of meat per can and the clams the lowest. The percentages of moisture, protein, carbohydrate, ash and calories per 100 grams of meat and liquor separately for the four species of shellfish are presented in table II.

TABLE II. The proximate analyses of canned crabs, shrimps and clams

Sample	Moisture (%)	Protein (%)	Fat (%)	Carbohydrate (%)	Ash (%)	Calories (per 100 g.)
Crabs						
Meat	76.6	20.2	1.5	....	1.7	96
Liquor	89.8	7.5	0.0	....	2.1	31
Shrimps						
Meat	74.9	19.9	1.8	....	3.4	97
Liquor	92.7	3.1	0.0	....	4.1	13
Clams (Butter)						
Meat	73.7	18.7	4.8	1.4	1.4	127
Liquor	93.5	3.5	0.0	1.9	1.1	22
Clams (Soft shell)						
Meat	78.5	15.6	2.5	1.7	1.7	89

The percentage of protein in the clams is slightly lower than that of crabs and shrimps. The percentage of fat in these shellfish doubtless depends largely on the season of catching and their treatment prior to canning. It is often the practice to hold crabs and clams without feeding in the salt water at the cannery for a few days and it is believed that this is a factor in reducing the fat stores.

No attempt was made in this work to follow the seasonal changes in the fat content of these shellfish. The nutritive value expressed as calories per 100 grams of canned crab, shrimp and clam meat is approximately 100 calories, and this value is similar to that obtained from the meat of non-oily fish, e.g. cod, haddock, halibut, etc.

A preliminary study of the vitamins A and D potency of the oil extracted from the viscera of crabs, using the methods described by Pugsley (1939), gave the following results: The six per cent of oil, that was obtained, contained vitamin A, 600 international units per gram, and vitamin D, less than 5 international units per gram.

ACKNOWLEDGEMENTS

The author is indebted to Mr. Hart of the Prince Rupert Canneries, Limited, for donating the samples of canned crabs, shrimps and butter clams, and to Mr. Hewson of Masset, B.C., for the soft-shelled clams used in this work.

REFERENCES

CARTER, N. M. *J. Biol. Bd. Can.*, **2**, (5), 439-455, 1936.
PUGSLEY, L. I. *J. Fish. Res. Bd. Can.*, **4**, (5), 396-404, 1939.
RIDDELL, W. R. *J. Biol. Bd. Can.*, **2**, (5), 463-475, 1936.
TULLY, J. P. *J. Biol. Bd. Can.*, **2**, (5), 477-484, 1936.
WHITE, F. D. *J. Biol. Bd. Can.*, **2**, (5), 457-462, 1936.

Variation of Vertebral Centra in Young Pacific Herring (*Clupea pallasii*)

By J. L. McHugh
Pacific Biological Station

(*Received for publication April 2, 1941*)

ABSTRACT

Structural variations in vertebral centra of young Pacific herring are described and classified. Evidence that "abnormal" centra are the result of fusion is brought forward, and the numerical value of complex segments is discussed. It is shown that populations may differ by the frequency with which vertebral irregularities appear, and that such differences may be associated with environmental factors. Fused centra tend to occur most frequently in the region of the twentieth vertebra, and this appears to be associated with differential growth in the vertebral column.

INTRODUCTION

An important operation in the investigation of the British Columbia herring fishery has been the statistical study of vertebral counts from random samples of spawning schools and of the commercial catch. By this method significant differences have been demonstrated between the runs to many localities (Tester 1937), and these differences have been interpreted as indicating a lack of free intermingling between these areas. In a similar study of the young fish taken during their first summer (Hart and McHugh 1939), the comparison of average vertebral counts has also suggested the existence of distinct populations, even within a limited area.

The number of vertebral centra occurring between, but not including, the basioccipital and the hypural bones has been adopted as the standard expression of the "number of vertebrae" of an individual. In a small but nevertheless distinct proportion of the vertebral columns, however, one or more complex centra may be found. Vertebrae of this type are apparently the result of either partial fusion or partial division of distinct centra, and since their origin has not been clearly understood, reliable counts are not possible from the individuals in which they appear. The existence of "abnormalities" of this nature has been recognized for some time, and it has been the practice in racial work to ignore the vertebral columns in which such irregularities appear. Schmidt (1921) contends that these individuals are just as "normal" as those in which no complex segments occur, and the rejection of specimens with "abnormal" vertebrae may introduce errors which will in turn lead to erroneous conclusions. Since the chief object of racial investigations on British Columbia herring has been to determine the extent of intermingling between fishing areas, it is necessary only to show

J. Fish. Res. Bd. Can. 5 (4) 1942
Printed in Canada

that differences between populations do exist. The reasons for such differences are of minor interest in this connection and their detection is unlikely to be affected greatly by the rejection of a small proportion of the data. Nevertheless, irregularities in centrum structure occur with sufficient frequency to justify a study of their structure and occurrence.

Several attempts have been made to determine the origin of complexities in centrum structure, or to assign numerical values to them, but the results of these efforts leave much to be desired. The present paper presents the results of a study of centrum variation in young Pacific herring, and points out certain features not previously described which seem to throw some light on the origin of so-called abnormalities.

MATERIALS AND METHODS

The samples of young herring from which the material for this study was obtained were collected mainly from waters in the southern part of the strait of Georgia. The vertebral columns were prepared for examination for the most part by maceration in thirty per cent alcohol. The softened tissues were teased away from the bony structures and the skeletons dried before examination. Specimens under thirty millimetres in length were found too delicate in structure for treatment by this method, and were accordingly stained and cleared by the alizarin method described by Hollister (1934).

The author wishes to thank Dr. J. L. Hart for permission to make use of material collected and prepared by him. The manuscript has been critically reviewed by various members of the staff of the Pacific Biological Station, and their suggestions are gratefully acknowledged.

CLASSIFICATION OF ABNORMALITIES

In practically all cases the abnormality is bilaterally asymmetrical, only 17 of 711 abnormal elements examined exhibiting bilateral symmetry. The number of abnormalities per skeleton ranged from one to seven, as shown by the following frequency distribution:

Number of abnormalities per vertebral column	0	1	2	3	4	5	6	7
Number of vertebral columns	6,845	343	90	41	9	2	2	1

The following types of complex vertebral elements have been recognized in the young Pacific herring, and are illustrated in figures 1 and 2.

Type 1

The most commonly observed type (63%) is that in which two adjoining centra are fused to some extent and exhibit bilateral asymmetry (fig. 1, a and b). Considerable variation in the completeness of the fusion has been encountered, and a complete series has been traced from a condition in which two centra are free on one side and slightly fused on the other to one in which a single centrum is apparently normal on one side and shows traces of a suture on the other.

Also included under type 1 are minor modifications of single centra. In some cases the centrum is reduced in length, one side being generally somewhat

shorter than the other. Cases of this kind are counted as normal vertebrae, but occasionally (2%) the centrum is so reduced that it disappears completely on one side of the fish, and becomes merely a wedge-shaped segment inserted between

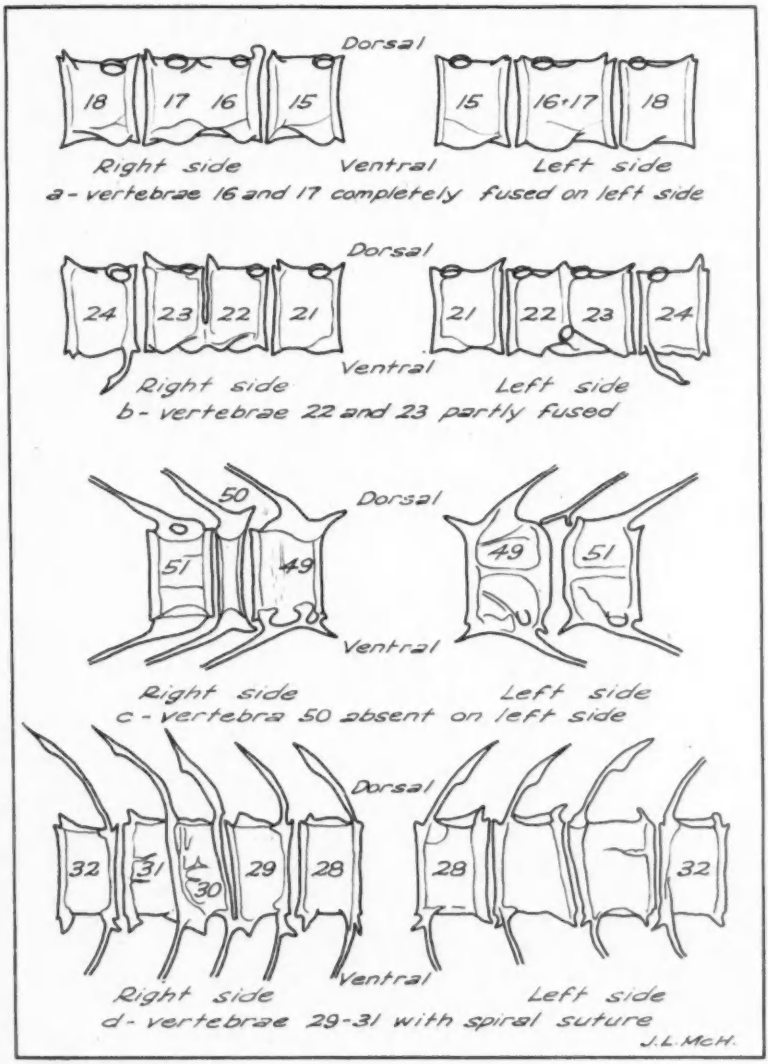

FIGURE 1. Types of abnormal centra found in young herring.

two vertebrae of normal length (fig. 1c). This may be free from or fused with the centra immediately anterior and posterior to it.

Very occasionally (less than 1%) the fusion of two centra may occur dorsally or ventrally rather than laterally, and the bilateral symmetry is therefore not disturbed.

One centrum was found to be incompletely calcified dorsally.

TYPE 2

Second in frequency of occurrence (22%) is a condition in which the suture between centra is not complete, and ends freely and abruptly on either the mid-dorsal or mid-ventral line (figs. 1d and 2a). The suture therefore takes the form of a spiral, and produces a complex centrum which on one side has the appearance of three somewhat short and distorted centra, and on the other side two rather elongate vertebrae.

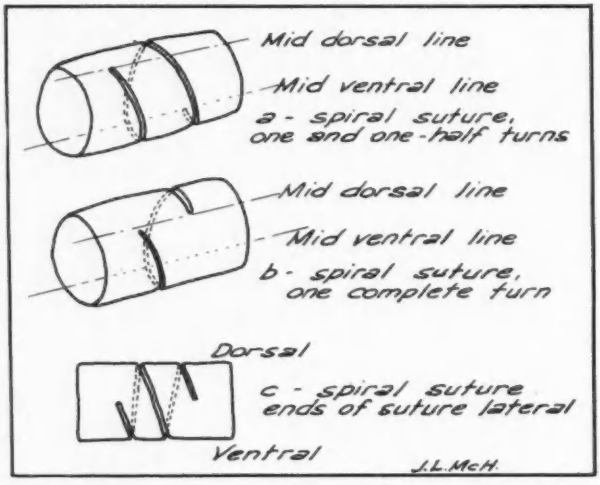

FIGURE 2. Diagrammatic representation of variations in abnormalities of type 2.

In a few instances the spiral completes one or more additional turns to produce either four centra on one side and three on the other (10 cases), or five and four respectively (2 cases).

In three instances an extra half turn added to or subtracted from the usual type of spiral caused both ends of the suture to end dorsally. In two the suture made a single turn, giving the appearance of two unequal centra on either side (fig. 2b). In one a spiral suture of two complete turns produced three distorted centra on each side.

Another modification of the spiral type of abnormality was observed in two cases. Here the ends of the suture were lateral rather than medial (fig. 2c).

TYPE 3

In eight per cent of the cases two or generally more consecutive centra were heavily ossified and rigidly fused with each other, but with the sutures fairly well

marked. In the majority of cases several or all of the vertebrae are somewhat distorted in shape, and the fused section is generally somewhat curved laterally. As many as twenty centra may be involved in an irregularity of this sort. Fourteen backbones gave a higher vertebral count on one side, and probably included an abnormality of type 1. Ten were cases of simple fusion of several adjoining vertebrae caused by unusually heavy ossification, and no departure from bilateral symmetry was evident.

TYPE 4

Compound vertebrae which are apparently bilaterally symmetrical appear very occasionally (1%). No excess ossification occurs and the sutures are less distinct than in type 3. Six were symmetrically double, and one quadruple.

TYPE 5

Associated with the abnormalities described above are various duplications and modifications of the neural and haemal arches and spines and of the other vertebral appendages, forming from 25 to 35 per cent of each sample. These modifications may also occur in association with "normal" centra, and as pointed out by Ford (1933) they are generally limited to the two vertebrae preceding the urostyle. Such cases are further distinguished from the so-called normal backbones by having a lower average vertebral count. Abnormalities of this type have not been considered as such in racial work because the centrum shows no sign of fusion, and except for table I, backbones of this type are included with the normal columns.

TABLE I. Frequency distributions of vertebral number for "normal" skeletons and skeletons containing abnormalities of type 5

Locality	Year		Frequency of vertebral columns with following number of centra							Mean
			48	49	50	51	52	53	54	
Fulford harbour	1932	Normal			3	48	124	38	3	51.95
		Abnormal	1		2	25	40	5	1	51.66
Fulford harbour	1935	Normal				12	49	6	1	51.94
		Abnormal				18	14			51.44
Fulford harbour	1937	Normal				13	46	14		52.01
		Abnormal			2	13	12			51.27
Nanoose bay	1934	Normal				18	43	13	1	51.96
		Abnormal			2	14	9			51.28
Ladysmith harbour	1937	Normal				19	44	11		51.89
		Abnormal			1	11	12	2		51.58
Departure bay	1939	Normal				8	48	9	4	52.13
		Abnormal				16	15			51.48

In table I are given the frequency distributions of vertebral number for "normal" skeletons and those having abnormalities of type 5. In each case the average for the latter is lower by approximately half a vertebra, which agrees with Ford's results for the European herring.

The artificial nature of the arbitrary groups set up for the classification of abnormalities is obvious. Wide variation occurs within a group, and a certain amount of overlapping between groups is unavoidable. Variations in abnormalities of type 1 present a complete series of intergrading forms bridging the gap between the extreme "abnormal" and the "normal" type (fig. 3). The fusion of two centra may be so slight as to be almost unnoticeable or so complete that only one vertebra appears to be present. Similarly, a single centrum may be found in all stages of reduction in size. Furthermore, it is probable that type 3 is

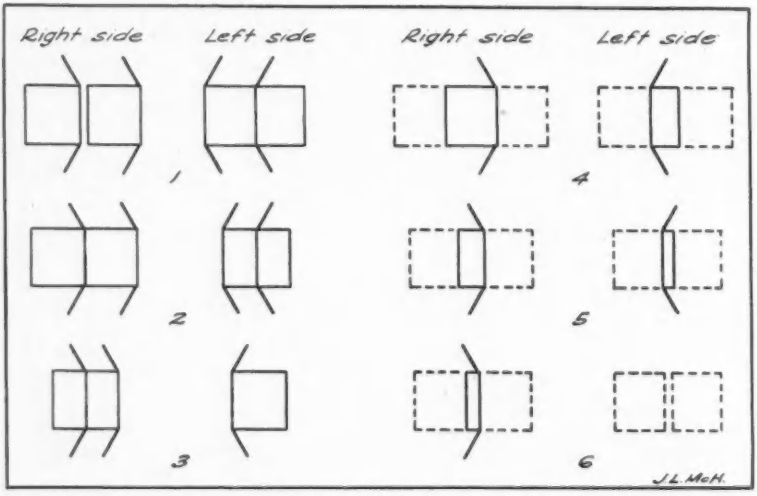

FIGURE 3. Diagrammatic representation of various stages of fusion between two adjoining centra (1-3) and of reduction in size of a single centrum (4-6).

merely a further modification of type 1 involving more than two vertebral elements, and that in type 4 a similar fusion has developed equally on both sides of the body. Variation in type 2 differs in that it apparently progresses by discrete steps.

ORIGIN OF ABNORMAL CENTRA

Attention should be drawn to the fact that in referring to complex centra the term "fusion" has been used. Apparently in the herring, abnormalities are the result of peculiarities in the development of the outer bony ring described by Gwyn (1940), since complex vertebral elements have not been observed in individuals in which only the inner bony ring of the centrum is formed. Figure 4 represents successive weekly samples from the same group of fish and shows that the proportion of abnormal vertebral columns increases in number as the post-

larvae increase in size. Unless the "abnormal" fish are subjected to a heavier mortality than the "normal" individuals, the incipience of complexities must cease with the completion of post-larval life, since at this stage abnormalities occur with approximately the same frequency as in the adult fish.

The incidence of peculiarities in structure of the outer bony rings might be brought about either by partial fusion or partial division of individual centra. Conclusive evidence is not available, but certain facts suggest that the process is one of fusion. In the youngest fish the elements involved in an abnormality tend to be rather lightly united and normal in size. A study of progressively older individuals shows an increase in the completeness of the association and a tendency for the elements to be shorter than the adjoining normal centra. Fusion is also suggested by the heavily ossified nature of many vertebral irregularities,

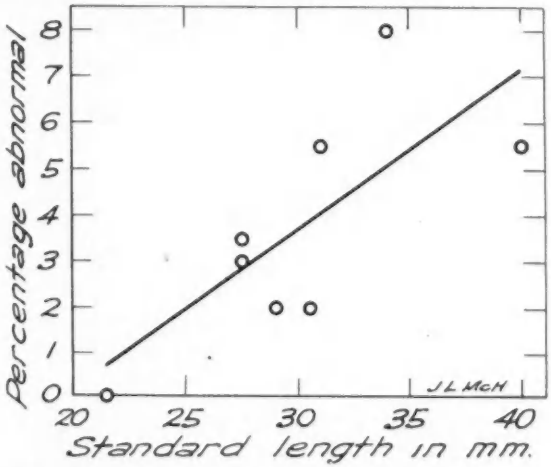

FIGURE 4. Increase in the percentage of abnormal vertebral columns per sample as the post-larvae increase in size.

showing that abnormality is generally associated with a greater bone-forming activity.

NUMERICAL VALUE OF ABNORMAL CENTRA

Attempts of other authors to define the numerical value of irregular vertebral elements have been prompted by their belief that elimination of abnormal skeletons from the calculations might lead to errors in the computation of the mean vertebral count. In spite of this belief some workers have assumed the mean value for the "normal" skeletons to be the correct one, and on this basis have developed correction factors which "restore" the normal count. Schmidt (1921) applied to each case of fused centra a value of $1\frac{1}{2}$, and Ford (1933) used this value for caudal centra having accessory processes, while Ford and Bull (1926) and Kandler (1932) considered each abnormality as a fusion of distinct vertebrae and counted it as such. The latter method seems logical in view of the above evidence

that abnormality is the result of fusion, but in the Pacific herring a similar treatment of the material produces values which are consistently high, as illustrated in table II. Since the fundamental causes of variation are unknown, no explanation other than a theoretical one is possible. But if the conclusions drawn in previous sections are reliable, and our estimates of the number of centra involved in each case are correct, then "abnormal" vertebral columns have on the average a higher count than "normal". On this basis the true vertebral number of a population would lie somewhere between the two values.

TABLE II. Average vertebral counts of "normal" and "abnormal" fish, each element involved in a fusion being counted as one centrum

Locality	Year	Average vertebral count		Difference
		Normal	Abnormal	
Departure bay	1932	51.68	51.87	+0.19
	1934	51.67	52.37	+0.70
	1937	51.85	52.21	+0.36
Nanoose bay	1934	51.72	52.38	+0.66
	1935	52.00	52.36	+0.36
	1936	51.84	52.38	+0.54
Fulford harbour	1932	51.88	52.28	+0.40
	1935	51.78	52.57	+0.79
	1937	51.82	52.38	+0.56
	1938	52.02	52.36	+0.34
Ladysmith harbour	1937	51.90	52.65	+0.75
Whaleboat passage	1938	51.77	52.29	+0.52
Ganges harbour	1938	51.77	52.18	+0.41
Deep bay	1939	51.96	52.33	+0.37
Active pass	1939	51.96	52.64	+0.68
Bidwell bay	1939	51.98	52.60	+0.62

LOCAL DIFFERENCES IN FREQUENCY OF ABNORMAL CENTRA

Kandler (1932), dealing with vertebral columns having duplicate processes in the last two centra as in type 5, has found that populations can differ by the frequency of their complex vertebrae. In young Pacific herring the proportion of vertebrae of this type remains fairly constant from sample to sample, but it has been observed that the percentage of backbones in which cases of fusion of types 1 to 4 are present varies considerably between samples. Approximately twelve per cent of fish taken in Nanoose and Departure bays (*a*) have cases of fusion in one or more sections of the vertebral column, while in all other localities (*b*) the proportion containing fused elements averages only five per cent. The actual percentages are (*a*) 14.0, 13.2, 13.0, 12.9, 11.7, 11.7, 9.0, 8.4, (*b*) 12.7, 8.5, 7.3, 6.7, 6.5, 6.2, 5.7, 5.2, 5.0, 4.2, 4.1, 3.9, 3.6, 2.7, 2.1, 2.0, 1.0. Statistical treatment of the two groups of samples shows that the difference is significant ($t = 5.92$; $P < 0.01$).

RELATION BETWEEN VERTEBRAL COUNT AND FREQUENCY OF ABNORMAL CENTRA

It was shown in the previous section that the percentage of vertebral columns containing cases of abnormality is significantly higher in the Departure-Nanoose bay area than in the other localities studied. Taking one locality in each area as an example, it is found that the average vertebral count of young herring taken in Departure bay over a period of eight years is 51.72, and this is significantly lower than the average value of 51.88 for samples captured in Fulford harbour over the same period. This would suggest that for these two localities the percentage of vertebral columns having abnormal centra is greatest in samples having a low mean vertebral number.

In figure 5 the percentage of vertebral columns containing abnormalities is plotted against the mean vertebral number for each sample. Samples composed of less than 100 fish are represented by blackened circles, since the values for

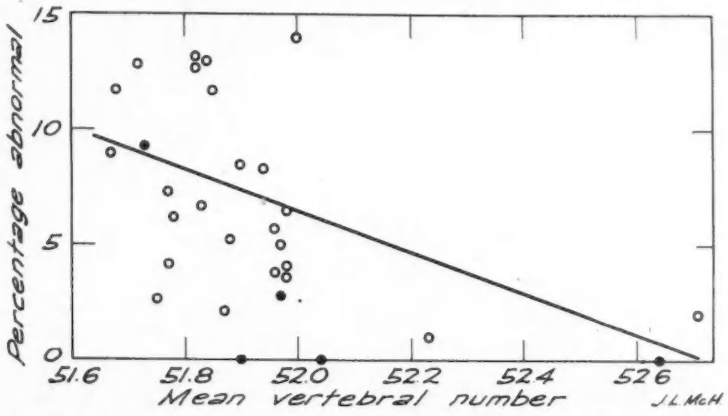

FIGURE 5. Relation between the percentage of abnormal vertebral columns and the mean vertebral number of each sample. Samples of less than one hundred fish represented by black circles.

percentage abnormality are considered less reliable. Considering all the data, a significant negative correlation can be established between per cent abnormality and mean vertebral count ($r = -0.497$; $t = -2.75$). Tester (1938) has shown for the Pacific herring that the mean vertebral count of successive year classes varies inversely with water temperatures during the period of spawning and early development. It would appear to follow that the proportion of abnormal skeletons per sample is highest when the temperature during the period of early development is relatively high. In rearing eggs of *Coregonus clupeaformis*, Price (1940) found that the number of deformed embryos produced increased from zero to one hundred per cent as the temperature was increased from 0.5 to 12 degrees Centigrade.

Summer water temperatures in the vicinity of Fulford harbour are known to be consistently lower than those in the Departure bay region (Hutchinson and

Lucas 1931). This is undoubtedly true also in the spring months, due to the greater instability of the water mass in the southern area, but no figures are available for the localities in which the young herring samples were captured. Excluding the data for small samples, and for those having counts higher than an average of 52 vertebrae, which is exceptionally high for the locality in question, the position and slope of the line fitted to the points by the method of least squares remain the same, but the correlation is no longer significant. However, the tendency remains for high vertebral counts to be associated with a low percentage of abnormal centra, and vice versa.

FREQUENCY OF ABNORMAL CENTRA ALONG VERTEBRAL COLUMN

Although complex centra have been observed in all parts of the vertebral column, a definite tendency is evident for abnormality to be localized in one

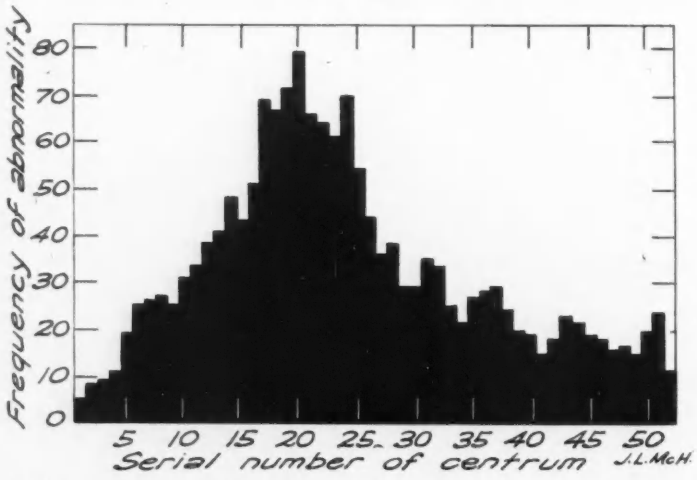

FIGURE 6. Relative frequency of occurrence of abnormality in each centrum of the vertebral column.

particular region. Ford and Bull (1926) found in *Clupea harengus* two regions in which such a concentration took place, and discovered that these corresponded to the positions traversed by the pelvic fins and the anus during metamorphosis. This they considered as an indication that differential growth may be responsible for the occurrence of fusion.

The frequency of abnormal centra in young *Clupea pallasii* is illustrated in figure 6. The serial positions of abnormal elements were arbitrarily defined by assigning a whole number to each unit involved in a fusion, and consequently each was considered as taking part in an abnormality. It is evident that in samples of this species taken in waters along the southeast coast of Vancouver island fusion takes place most frequently in the region of the twentieth vertebra.

In order to investigate the possibility that the phenomenon of abnormality

may be related to differential growth in the Pacific herring, a study was made of the movement of various points on the body of the developing post-larvae in relation to the vertebral column. The results of this investigation (fig. 7) show that during metamorphosis the pelvic fins move in a posterior direction from vertebra 22 to vertebra 26. At the same time the dorsal migrates in the opposite direction over an interval of eleven vertebrae (33 to 23), and the anus, the full range traversed by which cannot be stated, due to difficulty in making out the myomeres in the youngest fish, shifts anteriorly (43 to 38).

Comparing these regions with those in which abnormal centra occur most frequently, no relation is evident. Thus, although differential growth may be largely responsible for the production of abnormalities, there is no indication in

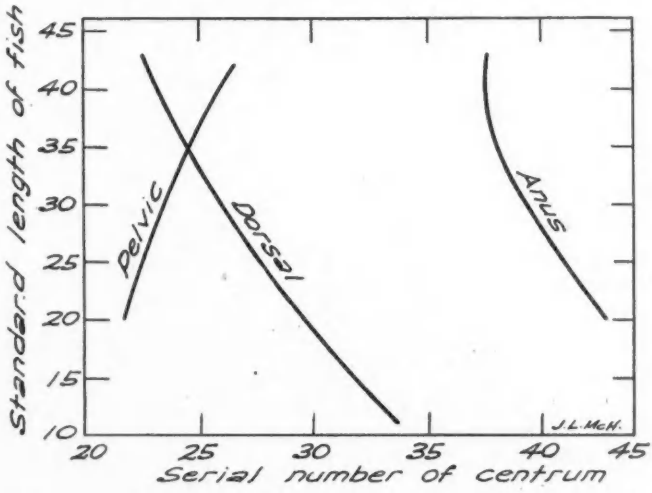

FIGURE 7. Movement of anus and of pelvic and dorsal fins in relation to the vertebral column during metamorphosis.

the Pacific herring that the movements of the fins are directly associated with the phenomenon.

RELATION BETWEEN VARIABILITY OF CENTRA AND FREQUENCY OF ABNORMAL VERTEBRAE

One of the most obvious characteristics of the vertebral column is the regular change in form of successive vertebrae. This heterogeneity of structure is related to the differential function of the various parts (Ford 1937). A less evident, but not unexpected feature is the variation in relative size and form of the same vertebra in different individuals. On the theory that variation in centrum length might be associated with the occurrence of abnormality, measurements were made of the lengths of individual centra in approximately one hundred young herring. It was found that the amount of variation in length of individual centra differed in different regions of the backbone, but that the standard deviation of

the length of an individual element was not a good measure of variability, since the relative length of a centrum changes as the fish increases in length. An index of variability was obtained by fitting a straight line to the length of fish—length of centrum relationship using the method of least squares, and by calculating the sum of the deviations from this line. Figure 8 presents the results of measurements of each individual vertebra for seventy-six individuals each having fifty-two vertebrae.

It was shown in the previous section (fig. 6) that fused vertebrae tend to occur most frequently at about the twentieth centrum. A comparison of figures 6 and 8 would suggest that an inverse relationship exists between the frequency of abnormality in any region of the vertebral column and the variability in centrum length in that region. A statistical treatment of the data shows that a highly significant correlation does exist ($r=0.548$; $P<0.01$).

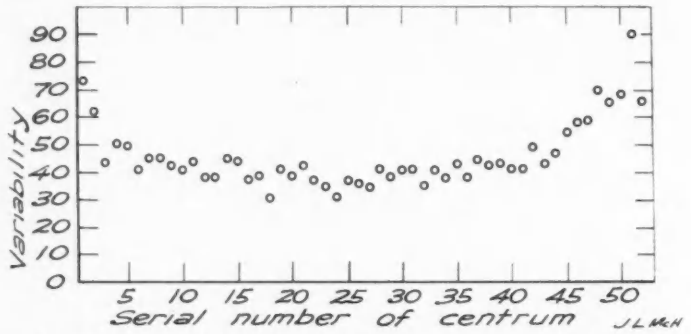

FIGURE 8. Relative variability in length of each centrum in samples of young herring.

DISCUSSION

Any explanation of the origin and development of abnormal vertebrae based on the preceding data must of necessity be highly hypothetical. For this reason, the theories here presented must be considered as the writer's interpretation of the results, with the realization that the evidence is purely circumstantial. Direct proof could best be obtained by experiment, but great difficulty has been experienced in holding herring in captivity.

The theory here postulated depends first on the previously discussed assumption that in *Clupea pallasii*, abnormalities are the result of fusion in the outer bony ring of the centrum. Gwyn (1940) indicates that the ends of the developing centra are separated by a thickening of the fibrous sheath of the notochord in the intervertebral regions, which pushes out laterally between the developing vertebrae. Ramanujam (1929) states that in *Clupea harengus* the bone-forming activity is greatest at the ends of the outer cylinder, and if this is true in the case of the Pacific herring, any disturbance retarding the thickening of the fibrous sheath in the intervertebral regions might be expected to bring the more rapidly-growing ends of the outer bony rings into close contact.

The structure of the fused segments examined, and the known facts concerning the early development of the vertebral column, seem clearly to point to differential growth as the causative agent. Miss Gwyn has pointed out that in the ossification of the inner bony rings of the vertebral column exclusive of the urostyle a definite growth-gradient exists, the first bone being laid down in the central portion of the backbone. Presumably these first-formed centra are limited in length by the gradual formation of bony rings in both a posterior and an anterior direction, building up a certain amount of internal compression which tends to reduce the variability of the individual elements. At the same time, pressures may be imagined as being exerted parallel to the long axis of the vertebral column by the presence of growth-gradients in the other body tissues. Pressure would provide an explanation of the mechanism by which the ends of the developing bony cylinders are brought in close contact, so that fusion might be mechanically possible. Compression of a rod-like structure such as the backbone will tend to cause buckling, and it is suggested that evidence for the presence of some such mechanical effect is provided by the almost universal occurrence of asymmetry in the cases of fusion observed in young herring.

Abnormalities of the spiral type are rather difficult to explain on the basis of fusion. However, it is possible that they may originate as the result of differential growth rates on opposite sides of the body, causing a displacement of the bone-forming tissues, generally along the mid-dorsal or mid-ventral line.

Irregularities of type 5 are apparently distinct from all other types for two main reasons. In the first place, no evidence of fusion is apparent in the centrum itself. Fortunately, the frequency of such cases is relatively constant, and therefore the error induced by their inclusion in the so-called normal group is probably not significant. In the second place, the phenomenon is associated with a low average vertebral count, in contrast to the high count described for other cases of fusion. However, a discrepancy must now be pointed out in the relation between frequency of abnormality and variability of centrum length. While the curve in figure 6 is fairly smooth in outline, that in figure 8 makes an abrupt drop from centrum 51 to 52, which is entirely opposite to the condition which might be expected if the inverse relationship holds. If, however, all cases of double spines are considered as fusions, the curve in figure 6 will make an equally abrupt rise in the position corresponding to the last vertebra, and the relationship between the two curves becomes more exact. The count for such vertebral columns must now be increased by one, which brings the count into correspondence with the high value encountered in other cases of fusion. The completeness of fusion, particularly in the most posterior centrum, may be brought about by factors similar to those which cause the posterior three bony rings to fuse, forming the urostyle.

SUMMARY

In the course of racial studies on young Pacific herring the attainment of accurate vertebral counts has been complicated in many cases by the occurrence of irregularities in centrum structure. A detailed study of these so-called "abnormalities" has shown that certain broad groups may be set up for their classifica-

tion. A further feature of importance is the asymmetrical nature of the phenomenon, the departure from normal being almost invariably more pronounced on one side of the fish.

Examination of various stages in the development of the post-larvae has led to the discovery that complex centra do not occur in the very young fish. The available evidence suggests that abnormality is the result of fusion.

Attempts to adjust the vertebral count of abnormal skeletons to that obtained from normal fish are criticised. It is pointed out that the "normal" value is not necessarily the true value for the mean vertebral count.

Certain populations have been shown to differ significantly in the frequency of occurrence of their complex vertebrae. The proportion of irregularities seems to be highest in samples with a relatively low mean vertebral number, and since vertebral number is known to vary inversely with water temperatures during early development, temperature may be a factor in the production of fused centra

An inverse correlation has been shown to exist between the frequency with which abnormalities occur in any particular centrum and the variability in length of that centrum. This seems to point to the phenomenon of differential growth as a prime factor in the production of abnormal vertebrae. Pressures set up by the action of growth-gradients in the development of the vertebral column and in the surrounding tissues provide a satisfactory explanation, which is supported by known facts concerning the structure and development of the centra.

REFERENCES

FORD, E. *J. Conseil*, **8**, (2), 211-222, 1933.
J. Mar. Biol. Ass., **22**, 1-60, 1937.
FORD, E., AND H. O. BULL. *J. Mar. Biol. Ass.*, **14**, 509-517, 1926.
GWYN, A. M. *J. Fish. Res. Bd. Can.*, **5**, (1), 11-22, 1940.
HART, J. L., AND J. L. MCHUGH. *Fish. Res. Bd. Can., Prog. Rep. Pac.*, **41**, 20-21, 1939.
HOLLISTER, G. *Zoologica*, **12**, (10), 89-101, 1934.
HUTCHINSON, A. H., AND C. C. LUCAS. *Canad. J. Res.*, **5**, 231-284, 1931.
KANDLER, R. *J. Conseil*, **7**, (3), 373-385, 1932.
PRICE, J. W. *J. Gen. Physiol.*, **23**, 449-468, 1940.
RAMANUJAM, S. G. M. *Proc. Zool. Soc. Lond.*, **25**, (3), 365-414, 1929.
SCHMIDT, J. *C.-R. Lab. Carlsberg*, **14**, (16), 1-5, 1921.
TESTER, A. L. *J. Biol. Bd. Can.*, **3**, (2), 108-144, 1937.
J. Conseil, **13**, (1), 71-75, 1938.

Sex Reversal In Individual Oysters

By Alfreda Berkeley Needler
Prince Edward Island Biological Station

(*Received for publication December 18, 1940*)

ABSTRACT

Among 57 individual oysters (*Ostrea virginica*) followed from 1932 to 1936, almost every variation occurs from no change in sex to change almost every year. High proportion of unchanging males suggests these as genetically males and the others with apparently random sex determination as hermaphrodites.

INTRODUCTION

It was proved in 1932 that oysters (*Ostrea virginica*) can change sex either from male to female or from female to male (Needler 1932b). This has since been confirmed by Burkenroad (1937) and Galtsoff (1937).

The writer is indebted to the Fisheries Research Board of Canada for providing facilities for the work at the Prince Edward Island Biological Station and to Dr. G. deB. Robinson and Dr. Daniel DeLury for valuable help in the statistical analysis of the data.

METHODS

In 1932 a number of oysters were drilled with a dentist's drill and their sex determined by examining a little of the gonad contents extracted with a pipette. The oysters chosen were two years old, a few three years old, but otherwise they were taken at random. They were marked in various ways and examined yearly. They were kept in wire baskets suspended from the Station landing stage where they seemed to grow normally and be healthy. It should be mentioned that abnormal sex ratios indicated that the oysters were living under unnatural conditions. The ratio of males to females increased slightly during the observations and there was a higher proportion of changes from female to male than from male to female. On the natural beds the ratio of males to females usually decreases as the oysters get older (Needler 1935). However, this would not invalidate the following conclusions. Of the original oysters some were lost in winter storms, a few died, and in a few the sex could not be determined one year. But records are complete for fifty-seven oysters.

OBSERVATIONS AND DISCUSSION

Table I summarizes these observations and shows that there is almost every variation from oysters which never change sex to those which change almost

J. Fish. Res. Bd. Can. 5 (4) 1942
Printed in Canada

TABLE I. Sex changes of individual oysters.

Number of individuals	1932	1933	—Year— 1934	1935	1936
17	♂	♂	♂	♂	♂
6	♂	♂	♂	♂	♀
1	♂	♂	♂	♀	♀
1	♂	♂	♂	♀	♂
2	♂	♀	♀	♀	♂
3	♂	♀	♀	♂	♂
1	♂	♀	♂	♂	♂
2	♀	♂	♂	♀	♂
1	♀	♂	♀	♂	♂
1	♀	♂	♀	♀	♂
1	♀	♂	♀	♀	♀
3	♀	♂	♂	♀	♀
3	♀	♂	♂	♂	♀
1	♀	♀	♂	♀	♀
2	♀	♀	♂	♂	♀
2	♀	♀	♀	♂	♀
5	♀	♂	♂	♂	♂
2	♀	♀	♀	♂	♂
1	♀	♀	♀	♀	♂
2	♀	♀	♀	♀	♀

every year. It is obvious that in many of the oysters the sex is determined afresh each year and that even six- and seven-year-old oysters are capable of changing sex.

It is impossible to know the sex of the oysters before 1932 but it is improbable that a significant number of those male in that year had been female before. Of these males seven were three years old and the remainder two years old. But it is known that less than 20 per cent of the oysters in the neighbourhood from which these were taken mature when one year old and only about 2 per cent produce eggs (Needler 1932a, 1935).

TABLE II. Sex changes of individual oysters (+, female to male; −, male to female).

Class I. (Males in 1932). Total changes, −14, +7.

								Totals
No.	17	6	1	1	2	3	1	31
1933.....	0	0	0	0	−2	−3	−1	−6
1934.....	0	0	0	0	0	0	+1	+1
1935.....	0	0	−1	−1	0	+3	0	−2, +3
1936.....	0	−6	0	+1	+2	0	0	−6, +3

Class II. (Females in 1932). Total changes, −16, +28.

														Totals
No.	2	1	1	1	3	3	1	2	2	5	2	1	2	26
1933.....	+2	+1	+1	+1	+3	+3	0	0	0	+5	0	0	0	+16
1934.....	0	−1	−1	−1	0	0	+1	+2	0	0	0	0	0	−3, +3
1935.....	−2	+1	0	0	−3	0	−1	0	+2	0	+2	0	0	−6, +5
1936.....	+2	0	+1	0	0	−3	0	−2	−2	0	0	+1	0	−7, +4

Table II is a re-statement of the data dividing the oysters into two classes according to whether they were male or female in 1932. Here "+1" represents a change from female to male, "−1" a change from male to female, and "0" an absence of change. The table shows that in class I there were 14 changes from male to female and 7 changes from female to male, while in class II there were 16 changes from male to female and 28 changes from female to male. In class I the number of possibilities for a change from male to female is the total of those oysters male in each year or 109 possibilities. Of these 109 possibilities 14 occur so the proportion of actual to possible changes is $14/109 = 0.128$. Again, in class I, the number of possibilities for a change from female to male is the total of those oysters female in each year or 15 possibilities and 7 changes actually occur. Thus the proportion of actual to possible changes is $7/15 = 0.467$. Similarly in class II the proportion of actual to possible changes from male to female is $16/47 = 0.340$ and from female to male is $28/57 = 0.490$. Thus the female to male proportions are very similar in the two classes but there is a considerable difference in the proportions of male to female changes. These proportions of changes from male to female may be repeated as follows:

In class I 14 changed, 95 did not change, or 109 altogether.
In class II 16 changed, 31 did not change, or 47 altogether.

In both classes 30 changed, 126 did not change, or 156 altogether. Application of the Chi-square test to these proportions gives a value for "P" of 4×10^{-4}. The tendency to change from male to female is significantly greater in class II than in class I although the tendency to change from female to male is similar in the two classes.

Now in class I there are 17 oysters that remained male throughout the period of observation. If these males are neglected and the proportions of changes calculated as before, the following results are obtained.

Number of changes male to female is	14
Number of changes female to male is	7
Number of possibilities for change male to female is	41
Number of possibilities for change female to male is	15
Proportion of changes male to female is	$14/41 = 0.342$
Proportion of changes female to male is	$7/15 = 0.467$

It has been shown that in class II the proportion of changes male to female is 0.340 and the proportion of changes female to male is 0.490. Thus if the 17 unchanged males be omitted there is a striking similarity in the proportion of changes in the two classes both from male to female and from female to male. This suggests that the 17 unchanged males may be different from the other males in the experiment and all the other oysters male and female in both classes may be regarded as belonging to a hermaphroditic group.

Coe (1932a) sectioned large numbers of oysters and found in *Ostrea lurida* that, besides specimens functioning as males with the growth of ovocytes arrested (hermaphroditic males), there were some in which the growth of ovocytes of the primary gonad was inhibited and histological examination showed practically no

ovocytes. He called these "true males". In *O. virginica* he found a separate group of males with very few ovocytes (Coe 1932b, 1934) and suggested that these might also be "true males". The unchanging males in the above experiment may well have been Coe's "true males".

REFERENCES

BURKENROAD, M. D. *J. Mar. Res.* **1,** 75-84, 1937.

COE, W. R. *Bull. Scripps Inst. Oceanog., Tech. Ser.* **3,** 119-144, 1932a.
Biol. Bull. **63,** 419-440, 1932b.
Amer. Nat. **68,** 1-16, 1934.
(paging as given in reprint)

GALTSOFF, P. S. *Collecting Net,* **12,** 187, 1937.

NEEDLER, A. B. *Contr. Canad. Biol. Fish.* **7,** 285-294, 1932a.
Prog. Rep. Atl. Biol. Sta. **5,** 3-4, 1932b.
Prog. Rep. Atl. Biol. Sta. **17,** 6-7, 1935.

Effect of Light on Copepods as Food for Passamaquoddy Herring

By W. H. Johnson
Department of Biology, University of Toronto, and
Woods Hole Oceanographic Institution.

(*Received for publication October 17, 1941*)

ABSTRACT

The copepods *Eurytemora herdmani*, *Tortanus discaudatus*, *Pseudocalanus minutus* and *Calanus finmarchicus* are stimulated to move upward by the decreasing light from the setting sun while they migrate downward by the increasing light from the rising sun. These responses to light govern, in part, their availability as food for the herring.

INTRODUCTION

It has been shown (Battle, Huntsman et al. 1936) that the principal food of the herring in the Passamaquoddy region, New Brunswick, consists of the free-swimming copepods that are common there, namely *Acartia clausi*, *Eurytemora herdmani*, *Tortanus discaudatus*, *Pseudocalanus minutus* and *Calanus finmarchicus*. Although the particular forms taken by the herring were found to be dependent to some extent upon their abundance, there was evidence that light may be an important factor. Therefore, studies were made of the effect of light on the vertical movements of *Eurytemora*, *Tortanus*, *Pseudocalanus* and *Calanus* (for *Acartia* see Johnson 1938), and of the food of the herring taken at different times of the day. An attempt is now made to relate the food of the herring to its vertical distribution (Johnson 1939a) as well as to that of the copepods. All samples were taken during the summers of 1934, 1935 and 1936.

EFFECT OF LIGHT ON VERTICAL DISTRIBUTION OF COPEPODS

Methods

The methods used for measuring light intensity, obtaining samples from different depths and for subsequently enumerating the copepods were as described for *Acartia* (Johnson 1938).

Results

Eurytemora herdmani

With *bright sun* on June 9, July 9, and September 2 (table I) the greatest numbers were near the bottom. At *dusk*, that is as full night approaches, on

J. Fish. Res. Bd. Can. 5 (4) 1942.
Printed in Canada

June 9 and September 2, the greatest numbers were at the surface, showing upward movements. When *starlight* and *moonlight* have continued for about two hours or more, there appears to be uniform distribution from the surface to the bottom, as on June 19, August 14, September 2 and 3.

At intermediate times, intermediate distributions are to be seen. Thus at

TABLE I. Numbers of *Eurytemora* taken at different depths under various conditions of light. Illumination is expressed as percentage of full noon June sunlight. "x" signifies presence of very small numbers.

	June 9, 1936, 3.30 p.m. Bright sun. 82.8% ill'n. Bain's island				June 9, 1936, 9.30 p.m. Dusk. Bain's island				June 10, 1936, 10.00 a.m. Weak sun. 34.3% ill'n. Bain's island			
Depth (m.)	0	2	7.5	15	0	2	7.5	15	0	2	7.5	15
Males.....	x	x	x	750	2200	x	x	300		200	400	200
Females...				200	600	x	x	x				x
Young....		x	450	1000	2600	150	250	200		200	450	200
	June 12, 1936, 4.30 p.m. Overcast. 11.4% ill'n. Bain's island				June 17, 1936, 5.00 a.m. Sunrise. 3% ill'n. Bain's island				June 19, 1936, 11.45 p.m. Starlight. Bain's island			
Depth (m.)	0	2	7.5	15	0	2	7.5	15	0	2	7.5	15
Males.....			x						600	550	900	150
Females...									200	150	600	300
Young....		800	1000	450			1000	300	750	1000	1300	1000
	July 9, 1936, 2.30 p.m. Bright sun. 68% ill'n. Big bay				July 31, 1936, 10.00 p.m. Full moon. Big bay				Aug. 1, 1936, 5.30 a.m. Sunrise. 2.9% ill'n. Big bay			
Depth (m.)	0	2	7.5	18	0	2	7.5	16	0	2	7.5	15
Males.....				400	1000	200	x	x				300
Females...					600			x			1600	x
Young....			400	700	3000	2800	1400	1000			1600	600
	Aug. 8, 1935, 11.30 a.m. Bright sun. 83% ill'n. Big bay				Aug. 8, 1935, 5.40 p.m. Sunlight. 27% ill'n. Big bay				Aug. 8, 1935, 8.55 p.m. Moon 2/3 full. Big bay			
Depth (m.)	0	2	10	16	0	2	10	19	0	2	10	18
Males.....			360	510			x	350	1250		x	
Females...			x	210			x	x		100	x	x
Young....		x	480	780			300	550	1900	600	240	
	Aug. 9, 1935, 12.10 a.m. Starlight. Big bay				Aug. 9, 1935, 6.25 a.m. ½ hr. after sunrise. Big bay				Aug. 14, 1936, 8.00 p.m. ½ hr. after sunset, Big bay			
Depth (m.)	0	2	10	16	0	2	10	20	0	2	7.5	15
Males.....	800			600			x	300	400	800	500	x
Females...	200							180	x	x		x
Young....	400		400				240	600	1600	1600	900	400

TABLE I—(*continued*)

	Aug. 14, 1936, 11.00 p.m. Starlight. Big bay				Aug. 16, 1934, 8.30 p.m. Dusk. Big bay				Aug. 16, 1934, 11.50 p.m. Starlight. Big bay			
Depth (m.)	0	2	7.5	15	0	2	20	40	0	2	20	40
Males.....	500	800	800	200	100	4600			x	500	x	
Females...	200		x	200	x	1200	200	100	100	200	150	110
Young....	900	1300	1500	1400	x	5400			x	2800	x	
	Aug. 27, 1935, 5.15 p.m. Fog. 3% ill'n. Big bay				Sept. 2, 1936, 10.00 a.m. Sunlight. 60% ill'n. Bain's island				Sept. 2, 1936, 2.00 p.m. Sun and occas. clouds. Bain's island			
Depth (m.)	0	2	10	18	0	2	7.5	15	0	2	7.5	15
Males.....		420	x	150			300	500	x	x	400	800
Females...		200	270	400			200	300		x	x	200
Young....		460	120	100			600	1200		700	500	1200
	Sept. 2, 1936, 6.15 p.m. Sunlight. 7% ill'n. Bain's island.				Sept. 2, 1936, 7.30 p.m. Dusk. Bain's island				Sept. 2, 1936, 11.30 p.m. Full moon. Bain's island			
Depth (m.)	0	2	7.5	15	0	2	7.5	18	0	2	7.5	18
Males.....		x	x	200	500	200	300	150	400	300	300	200
Females...			x	x	300	100	200		150	200	200	
Young....		300	300	600	900	800	600	400	700	500	600	500
	Sept. 3, 1936, 3.20 a.m. Full moon. Bain's island				Sept. 3, 1936, 6.00 a.m. Sunrise. 3% ill'n. Bain's island				Sept. 3, 1936, 10.00 a.m. Sunlight. 60% ill'n. Bain's island			
Depth (m.	0	2	7.5	15	0	2	7.5	15	0	2	7.5	15
Males.....	300	300	400	400		150	500	750			200	600
Females...	150	150	150	x		150	350	500			200	550
Young....	600	600	600	600		300	500	650		x	500	600
	Sept. 13, 1935, 7.20 p.m. Sunset. 3% ill'n. Big bay				Sept. 13, 1935, 10.20 p.m. Full moon. Big bay							
Depth (m.)	0	2	10	16	0	2	10	16				
Males.....	270	450	100	800	700	2400	1000	300				
Females...	210	100	x	300	450	800	800	1500				
Young....	420	600		800	1850	1200	1800	600				

sunrise, that is between moonlight or starlight and sunlight on June 17, August 1 and September 3, the movement downward had occurred as shown by none being found at the surface and a few at 2 metres depth, but the greatest numbers were usually at the mid-level of 7.5 metres rather than the bottom (as found later) as would be expected if they were moving downward from the upper levels with increasing light. Again shortly after *sunset*, that is between sunlight and dusk, on August 14 and September 13 there were some at the surface, showing upward

movement from the sunlight condition, but it cannot be said that they were yet concentrated there.

In the morning with *weak sunlight* on June 10, and in the afternoon with an overcast sky on June 12, they were nearer the surface and less concentrated at the bottom than would otherwise be expected at such times, presumably due to the lower intensity of light. With occasional clouds, and therefore changing but not very low light intensity, some were near or even at the surface, although the greatest concentration was near the bottom.

No significant differences can be seen between males, females and young.

Tortanus discaudatus

At all times *between sunrise and sunset* (table II, July 8, 9 and 13, August 4, 8, 9, 23 and 27), whether or not the sun was hidden by clouds or fog, the animals were largely confined to the deep water.

TABLE II. Numbers of *Tortanus* taken at different depths under various conditions of light

	July 8, 1936, 3.30 p.m. Occas. clouds, 57 & 14%. Big bay				July 9, 1936, 2.30 p.m. Sunlight. 68% ill'n. Big bay				July 13, 1936, 5.00 p.m. Overcast. Big bay			
Depth (m.)	0	2	7.5	18	0	2	7.5	18	0	2	7.5	16
Males.....				200				200				
Females...												
Young....			600	x			3000	1800			400	1000
	July 31, 1936, 10.00 p.m. Full moon. Big bay				Aug. 4, 1936, 10.30 a.m. Overcast. 5% ill'n. Big bay				Aug. 8, 1935, 11.30 a.m. Sunlight. 83% ill'n. Big bay			
Depth (m.)	0	2	7.5	16	0	2	7.5	16	0	2	7.5	16
Males.....		x	200	175			x	1500			840	300
Females...											180	150
Young....	200	800	1300	660						150	1300	400
	Aug. 8, 1935, 2.40 p.m. Sunlight. 75% ill'n. Big bay				Aug. 8, 1935, 5.40 p.m. Sunlight. 27% ill'n. Big bay				Aug. 8, 1935, 8.55 p.m. Moon 2/3 full. Big bay			
Depth (m.)	0	2	10	18	0	2	10	19	0	2	10	18
Males.....		?	750	450			200	700	3900	1700	x	x
Females...		?	300	150					700	500	x	x
Young....		?	2150	800		x	450	150	2000	1000	1260	x
	Aug. 9, 1935, 12.10 a.m. Starlight. Big bay				Aug. 9, 1935, 3.20 a.m. Starlight. Big bay				Aug. 9, 1935, 6.25 a.m. ½ hr. after sunrise. 3% Big bay			
Depth (m.)	0	2	10	16	0	2	10	18	0	2	10	20
Males.....	600	200	800	600	400	600	600	400			360	780
Females...	400	100	1000	800	1000	1200	1000	600			120	180
Young....	1000	100	1000	800	1000	1000	1200	1000		x	1140	240

TABLE II—(*continued*)

	Aug. 14, 1936, 8.00 p.m. Dusk. Big bay				Aug. 16, 1934, 8.30 p.m. Dusk. Inner bay				Aug. 16, 1934, 11.50 p.m. Starlight. Inner bay			
Depth (m.)	0	2	7.5	15	0	2	20	40	0	2	20	40
Males.....	900	x	x	x	220	400	x	x	x		x	
Females...					230	200	770	740	210	200	260	280
Young....	x	300	1600	200	x	200	x	160				
	Aug. 23, 1935, 11.30 a.m. Overcast. 25% ill'n. Big bay				Aug. 27, 1935, 5.15 p.m. Fog. 3% ill'n. Big bay				Aug. 27, 1935, 8.00 p.m. Dusk and foggy. Big bay			
Depth (m.)	0	2	10	18	0	2	10	18	0	2	10	18
Males.....			120	240		240	200	200	900	250	360	120
Females...			x	270		180	180	350	x	200	240	180
Young....		220	1000	900	110	200	960	300	1000	1000	990	270
	Sept. 3, 1935, 7.50 p.m. Dusk. Big bay				Sept. 13, 1935, 10.20 p.m. Full moon. Big bay				Sept. 14, 1935, 1.20 a.m. Full moon. Big bay			
Depth (m.)	0	2	10	16	0	2	10	16	0	2	10	16
Males.....	1240	900	900	400	1250	1000	1100	1100	1600	1750	1600	1500
Females...		100	240	220	750	800	600	200	900	700	750	800
Young....	x	100	900	300	750	800	600	600	1000	900	1250	1000

Just after sunset (between ca. 8.00 and 9.00 p.m. on August 8, 14, 16 and 27, and September 3), however, upward migration to the surface occurred, the copepods being found at all depths. It is interesting to note that except in one instance the animals were not concentrated at the surface as was the case with *Eurytemora* under such light conditions. Samples taken under *starlight and moonlight* at later times during the night (between 10.00 p.m. and 3.20 a.m. on July 31, August 9 and 16, and September 13 and 14) showed the copepods to be uniformly distributed at all depths.

As was the case with *Eurytemora*, no significant differences can be seen between males, females and young.

Pseudocalanus minutus

All samples taken under the bright illumination occurring throughout the *day-time* but before sunset (table III, June 9, 10 and 17, July 8 and 9, August 1, 8, 9, and 27, and on September 2 and 3) showed the copepods to be mostly limited to the deep water.

Under rapidly decreasing light intensity in the *evening* at the time of and shortly following sunset (June 9, and on September 2 and 13), marked upward migration to the surface occurred. Tows taken later at night and under the weaker illumination of *starlight* and *weak moonlight* (August 8 and 9) showed no noteworthy concentration occurring at any particular depth. Such a uniform vertical distribution at night also occurred under long continued light from the

full moon (July 31 and September 2) although the copepods were apparently first repelled from the immediate surface at 10.00 p.m. on July 31 and at 11.30 p.m. on September 2 as the moon was rising in elevation.

No very significant differences in behaviour between males, females and young were noted,

TABLE III. Numbers of *Pseudocalanus* taken at different depths under various conditions of light.

	June 9, 1936, 3.30 p.m. Sunlight. 82% ill'n. Bain's island				June 9, 1936, 9.30 p.m. Dusk. Bain's island				June 10, 1936, 10.00 a.m. Sunlight. 34% ill'n. Bain's island			
Depth (m.)	0	2	7.5	15	0	2	7.5	15	0	2	7.5	15
Males.....				200	250					x	x	x
Females...			x	x	x						x	x
Young....			x	160	350	x	x	x		x	200	x
	June 17, 1936, 5.00 a.m. Sunrise. 3% ill'n. Bain's island				July 8, 1936, 3.30 p.m. Occas. clouds. Big bay				July 9, 1936, 2.30 p.m. Sunlight. 68% ill'n. Big bay			
Depth (m.)	0	2	7.5	15	0	2	7.5	18	0	2	7.5	18
Males.....	x	x	x	1100				x				800
Females...			x	150				x			x	x
Young....		x	x	300				850			400	1200
	July 31, 1936, 10.00 p.m. Full moon. Big bay				Aug. 1, 1936, 5.30 a.m. Sunrise. 3% ill'n. Big bay				Aug. 8, 1935, 5.40 p.m. Sunlight. 27% ill'n. Big bay			
Depth (m.)	0	2	7.5	16	0	2	7.5	15	0	2	10	19
Males.....		500									200	450
Females...		400									100	100
Young....		1000		x			500	1000			1000	2100
	Aug. 8, 1935, 8.55 p.m. Moon 2/3 full. Big bay				Aug. 9, 1935, 12.10 a.m. Starlight. Big bay				Aug. 9, 1935, 3.20 a.m. Starlight. Big bay			
Depth (m.)	0	2	10	18	0	2	10	16	0	2	10	18
Males.....	100	100	120	100	150	x	200	100	100	100	200	100
Females...	600	400	210	800	800	100	600	200	300	200	300	200
Young....	x	x	120	150	150	100	200		150	160	200	150

Calanus finmarchicus

This copepod was found to be very scarce within Inner Passamaquoddy bay, to which body of water the studies were largely confined. Some young of this species were found, however, and their vertical distributions determined at approximately three-hour intervals during the course of one day.

At all times under bright *sunlight* (table IV, August 8 and 9) the copepods were entirely limited to the deep water (from 10 metres to the bottom). Tows taken at 8.55 p.m. under the light from the *moon* (two-thirds full) showed that

TABLE III—(*continued*)

Depth (m.)	Aug. 9, 1935, 6.25 a.m. Sunlight. 3% ill'n. Big bay 0	2	10	20	Aug. 27, 1935, 5.15 p.m. Fog. 3% ill'n. Big bay 0	2	10	18	Sept. 2, 1936, 10.00 a.m. Sunlight. 60% ill'n. Bain's island 0	2	7.5	15
Males.....			240	960			130	x			x	750
Females...			120	360			120	x				750
Young....			390	2400		150	150	300			400	1050
	Sept. 2, 1936, 2.00 p.m. Occ. clds. 78 & 28% ill'n. Bain's island				Sept. 2, 1936, 6.15 p.m. Sunlight. 7% ill'n. Bain's island				Sept. 2, 1936, 7.30 p.m. Dusk. Bain's island			
Depth (m.)	0	2	7.5	15	0	2	7.5	16	0	2	7.5	18
Males.....	x		x				x	x	800	x	x	x
Females...	x		x	x					200	x	x	
Young....		400	x	400		400	550	650	2700	400	400	400
	Sept. 2, 1936, 11.30 p.m. Moonlight. Bain's island				Sept. 3, 1936, 3.30 p.m. Moonlight. Bain's island				Sept. 3, 1936, 6.00 a.m. Sunrise. 3% ill'n. Bain's island			
Depth (m.)	0	2	7.5	18	0	2	7.5	15	0	2	7.5	15
Males.....	x	450	150	x	300	300	300	150			x	900
Females...	x	150	x		x	x	x	x	x	x	x	300
Young....	600	1200	750	450	600	600	700	400			800	1800
	Sept. 3, 1936, 10.00 a.m. Sunlight. 60% ill'n. Bain's island				Sept. 3, 1935, 7.50 p.m. Dusk. Big bay				Sept. 13, 1935, 7.20 p.m. Sunset. 3% ill'n. Big bay			
Depth (m.)	0	2	7.5	15	0	2	10	16	0	2	10	16
Males.....			x	900					130	150		
Females...			x	450	x		x	x				
Young....			400	1350	x	300	120	x	400	200	x	500

the animals had extended up to the surface, which does not agree with the vertical distribution found in 1933 (Battle, Huntsman et al. 1936) when this copepod was found to be repelled from the surface; in the latter case, however, the moonlight was somewhat brighter.

Samples obtained later in the night under *starlight* (12.10 and 3.20 a.m.) indicated the animals to be uniformly distributed at all depths. The light from the rising sun evidently again drove them downwards as shown by the fact that at one-half hour after *sunrise* they were in greatest numbers close to the bottom.

FOOD OF HERRING IN RELATION TO LIGHT

METHODS

Samples of herring were obtained during the summer of 1936 from herring weirs (while being seined by the fishermen) and by means of gill nets used to determine the vertical distribution of the fish (Johnson 1939a). The stomachs

TABLE IV. Numbers of young *Calanus* taken at different depths under various conditions of illumination in Big bay

Depth (m.)	Aug. 8, 1935, 8.20 a.m. Sunlight. 37% ill'n.				Aug. 8, 1935, 11.30 a.m. Sunlight. 83% ill'n.				Aug. 8, 1935, 2.40 p.m. Sunlight. 75% ill'n.			
	0	2	10	18	0	2	10	16	0	2	10	18
			?	1400			1470	2640		?	600	800
Depth (m.)	Aug. 8, 1935, 5.40 p.m. Sunlight. 27% ill'n.				Aug. 8, 1935, 8.55 p.m. Moon 2/3 full.				Aug. 9, 1935, 12.10 a.m. Starlight.			
	0	2	10	19	0	2	10	18	0	2	10	16
			950	1700	450	500	720	850	450	600	500	700
Depth (m.)	Aug. 9, 1935, 3.20 a.m. Starlight.				Aug. 9, 1935, 6.25 a.m. Sunlight. 3% ill'n.							
	0	2	10	18	0	2	10	20				
	900	1000	1000	900			370	3340				

were removed, preserved in four per cent formaldehyde, and the contents later identified and counted.

RESULTS AND DISCUSSION

In the results of the stomach analyses (table V), the fish are classified according to their length, i.e. whether "brit", "snippers", "oils", "mustards" or "stringers" (for actual lengths see Johnson 1939a; "brit" are the shortest and "stringers" the longest).

HERRING OBTAINED FOLLOWING DARK NIGHTS

Laboratory experiments (Johnson 1939b) indicated that the absence of appreciable light on dark nights (foggy, cloudy, or starlight) prevents the herring from feeding since the fish are unable to see their food. Herring removed from weirs some time in the morning may or may not have entered before daybreak and been unable to feed thereafter. Although some of the samples thus obtained following dark nights contained food (June 9, 19, September 4, 11, 12, 21, 22, and 23) feeding may have taken place between dawn and the time when the fish were taken from the water. Quite a number of the samples of both small and large herring were found to contain no food (June 9, and September 10, 19, and 24) even though, as already seen, the copepods may be found at all levels during such dark nights.

HERRING OBTAINED IMMEDIATELY FOLLOWING MOONLIGHT NIGHTS

It was found in the laboratory that bright moonlight is of sufficient intensity to enable the herring to feed (Johnson 1939b). Examination of the stomachs of fish taken from the sea confirmed this observation. Two samples were obtained when the moon was two-thirds full (Spectacles island on June 10, and Bain's island on September 5). In the first instance some "brit" were found containing *Pseudo-*

calanus, *Acartia* and *Eurytemora*, and in the second instance some of the "snippers" contained *Pseudocalanus* and *Eurytemora* with the "oils" containing some *Calanus*. The presence of these copepods at the surface under such light has been shown.

TABLE V. Average percentages of various food animals in stomachs of herring taken under different conditions of light

Place, date, etc.	Illumination		Size of fish	*Calanus*	*Pseudocalanus*	*Acartia*	*Tortanus*	*Eurytemora*
	When taken	Previously						
Simpson id.	Foggy	Foggy	Snippers	–	–	–	–	–
June 9			Oils	–	–	–	–	–
7.30 a.m.			Mustards	–	–	–	–	–
Mowat id.	Foggy	Foggy	Oils	85	15	–	–	–
June 9								
7.30 a.m.								
Spectacles ids.	Sunlight	Moonlight	Brit	–	25	50	–	25
June 10		(previous	Snippers	–	–	–	–	–
8.30 a.m.		night)	Oils	–	–	–	–	–
Partridge id.	Foggy	Foggy	Brit	–	–	–	50	50
June 11			Snippers	–	–	–	–	–
9.30 a.m.			Oils	–	–	–	–	–
June 12	Foggy	Foggy	Brit	–	–	72	–	28
10.00 p.m.			Snippers	–	–	40	–	60
			Oils	40	–	60	–	–
Bain's id.	Sunlight	Sunlight	Snippers	–	–	40	–	60
June 17			Oils	100	–	–	–	–
3.30 p.m.								
Simpson's id.	Sunlight	Sunlight	Snippers	–	–	–	–	–
June 17			Oils	–	–	–	–	–
3.30 p.m.			Mustards	–	–	–	–	–
			Stringers	–	–	–	–	–
Dinner id.	Cloudy	Cloudy	Snippers	91	2	–	–	7
June 19			Oils	100	–	–	–	–
5.30 a.m.								
Partridge id.	Cloudy	Cloudy	Brit	–	–	–	–	100
June 19			Snippers	75	–	–	–	25
5.00 a.m.			Oils	–	–	–	–	–
St. Helena id.	Bright	Moonlight	Snippers	45	3	43	3	6
Aug. 23	sunlight	(previous	Oils	89	–	2	–	9
Noon		night)	Mustards	–	–	–	–	–
Aug. 24	Bright	Moonlight	Snippers	38	8	33	8	13
1.00 p.m.	sunlight	(previous	Oils	99	–	1	–	–
		night)						

TABLE V—(*continued*)

Place, date, etc.	Illumination		Size of fish	*Calanus*	*Pseudocalanus*	*Acartia*	*Tortanus*	*Eurytemora*
	When taken	Previously						
Partridge id. Sept. 1 5.00 a.m.	Moonlight	Moonlight	Oils	60	–	20	–	20
Bain's id.	Sunrise	Moonlight	Brit	–	58	26	–	16
Sept. 3			Snippers	100	–	–	–	–
6.30 a.m.			*Oils	100	–	–	–	–
			*Mustards	–	–	–	–	–
			*Stringers	–	–	–	–	–
Sept. 4	Overcast	Cloudy night	Snippers	73	21	–	–	6
8.15 a.m.			Oils	96	2	2	–	–
Sept. 5	Sunrise	Moonlight	Snippers	–	60	–	–	40
6.00 a.m.			Oils	100	–	–	–	–
St. Helena id. Sept. 9 9.00 a.m.	Overcast	Overcast	Oils	55	15	10	–	20
Partridge id. 12.00 noon Sept. 9	Foggy	Foggy	Brit	–	–	16	–	84
St. Helena id. Sept. 10 9.00 a.m.	Foggy	Overcast	Oils	–	–	–	–	–
Sept. 11 6.00 a.m.	Foggy	Starlight	Oils	98.0	–	0.5	–	1.5
Sept. 12 6.00 a.m.	Foggy	Foggy	Oils	98.0	–	0.5	–	1.5
Brandy cove Sept. 19 9.00 a.m.	Overcast	Overcast	Oils	–	–	–	–	–
Sept. 21 9.00 a.m.	Overcast	Overcast	Oils	–	–	85	5	10
Sept. 22 9.00 a.m.	Overcast	Overcast	Oils	–	–	–	20	80
Sept. 23 9.00 a.m.	Overcast	Overcast	Oils	–	–	77.5	7.5	15
Sept. 24 10.00 a.m.	Overcast	Overcast	Oils	–	–	–	–	–

**Meganyctiphanes* (Euphausiid shrimp) in their stomachs.

HERRING OBTAINED DURING BRIGHT SUNLIGHT

As already indicated, under bright sunlight the copepods are all largely limited to the deep water from 7.5 metres to the bottom. Even the largest herring that come into consideration are, under such light conditions, as near to the surface as three metres at mid-day, although their lower limits cannot be specified

(Johnson 1939a) and so it cannot be stated with certainty whether or not the food would be available to the fish at such times. Herring taken under bright sunlight (June 17 at Bain's island and August 23 at St. Helena island) contained less food, and that in a more advanced state of digestion, when taken late in the day as compared with those taken early in the day or with those taken late on moonlight nights or at sunrise, possibly indicating that the descent of the food below the fish prevented feeding under very bright sunlight. Too much significance cannot be placed upon these results, however, since herring held within weirs reportedly do not feed even when food is available. A further complicating factor is the presence in parts of Passamaquoddy bay of strong tidal currents which keep the copepods at all depths, making them always available to the fish at any depth—a fact which must be borne in mind when attempting to explain the role played by any condition of light. Furthermore, the presence of enemies such as mackerel and squid will prevent herring from feeding.

CONCLUSIONS

As was found to be the case for *Acartia* (Johnson 1938), upward migration by *Eurytemora*, *Tortanus*, *Pseudocalanus* and *Calanus* occurred in the evening as the light was decreasing in intensity, while downward migration took place in the morning about time of sunrise as the light was increasing in intensity. *Acartia*, however, was repelled by sunlight to a lesser extent than the other forms.

As was found for *Acartia*, uniform vertical distributions of all species occurred at night.

No marked differences in behaviour between males, females and young were noted.

As to the manner by which light controls the vertical distribution of the copepods, changing light intensity seems to be the stimulus for migration, the animals moving toward the light when the intensity is decreasing while moving away from the light when its intensity is increasing,—observations previously reported for *Acartia* (Johnson 1938).

The occurrence of different amounts and kinds of copepods in herring stomachs under different conditions of light can be explained by: (*a*) the time when the fish were captured, (*b*) the light conditions preceding the time of capture, (*c*) the actual vertical distributions of both the herring and the copepods under different conditions of light, and (*d*) the rate of digestion of the food.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to Dr. A. G. Huntsman of the Fisheries Research Board of Canada for stimulating the investigation in many ways; to Dr. A. H. Leim and Mr. E. G. Rigby for placing the facilities of the Atlantic Biological Station at the writer's disposal. The investigation was financed by the Dept. of Biology of the University of Toronto, the Biological Board (now the Fisheries Research Board) of Canada and the Woods Hole Oceanographic Institution.

REFERENCES

BATTLE, H. I., A. G. HUNTSMAN, A. M. JEFFERS, G. W. JEFFERS, W. H. JOHNSON, AND N. A. MCNAIRN. *J. Biol. Bd. Can.*, **2** (4), 401-429, 1936.

JOHNSON, W. H. *Biol. Bull.*, **75** (1), 106-118, 1938.

J. Fish. Res. Bd. Can., **4** (5), 349-354, 1939a.

J. Fish. Res. Bd. Can., **4** (5), 392-395, 1939b.

The Waters of the Scotian Shelf

By H. B. Hachey
Atlantic Biological Station

(Received for publication July 26, 1940; revised by the editor, the author being on active military service)

ABSTRACT

In the waters of the Scotian shelf there are: An "upper" layer with temperature in summer above and in winter below 5°C., and with salinities always less than 32 ‰; an "intermediate" layer with temperature generally below 5° and with salinities between 32 and 33.5 ‰; and a "bottom" layer with temperature above 5° and salinities above 33.5 ‰.

From 1934 to 1939, 1934 was the warmest and 1935 the coldest year in these waters. The submarine physiography of the shelf is important in preventing interchange between the deeper waters at the northeast and the remainder.

The submarine physiography of the continental shelf to the southeast of Nova Scotia delineates an area that has been termed the Scotian shelf (Hachey 1937a). The first detailed hydrographical examination of the waters of this area was made by the Canadian Fisheries Expedition of 1914-15 (Bjerkan 1919). Since 1932, the Fisheries Research Board of Canada has been giving attention to various oceanographical problems of the area, and a description of certain outstanding features has already been published (Hachey 1934, 1935a, 1935b, 1937b, 1938; Leim and Hachey 1935). The present paper presents an analysis of selected data to outline the more general features of the waters of the Scotian shelf.

MATERIAL

A network of stations (fig. 1) was established on the Scotian shelf in 1934. Material from these was obtained by the Atlantic Biological Station's boat "Zoarces", but for winter observations C.G.S. "Arleux" and C.G.S. "Arras" were used. Temperature and salinity observations were made at these at serial depths (0, 10, 25, 50, 75, 100, etc. metres) in both spring and summer from 1934 to 1938, and as well at other seasons, particularly in winter, in certain years, including 1939. There has also been available material obtained rather frequently from 1932 to 1935 (representative winter observations only in 1935) at station 60, lat. 44°23′25″N. and long. 63°21′58″W., which is in 100 metres of water off Halifax near station 58.

For the area as a whole the seasonal changes will be illustrated by the distribution of temperature and salinity found in 1938 in winter (January 24 to 29), spring (April 26 to May 3), and summer (August 26 to 30), and the annual changes

J. Fish. Res. Bd. Can. 5 (4) 1942
Printed in Canada

by such data obtained in spring (May 6 to 10 and May 15 to 21) and summer (August 8 to 12 and August 26 to 30) in 1934 and 1935 respectively. The changes in the inshore waters can be followed at more frequent intervals in the data for station 60, and those of the offshore waters in data for stations 125 and 128 from April 28, 1936, to February 9, 1937.

THE AREA AS A WHOLE

Changes from Season to Season

as shown vertically

The *winter* condition is shown in figures 2 and 3. The sections may be orientated by reference to figure 1, and it will be noted that the upper four sections

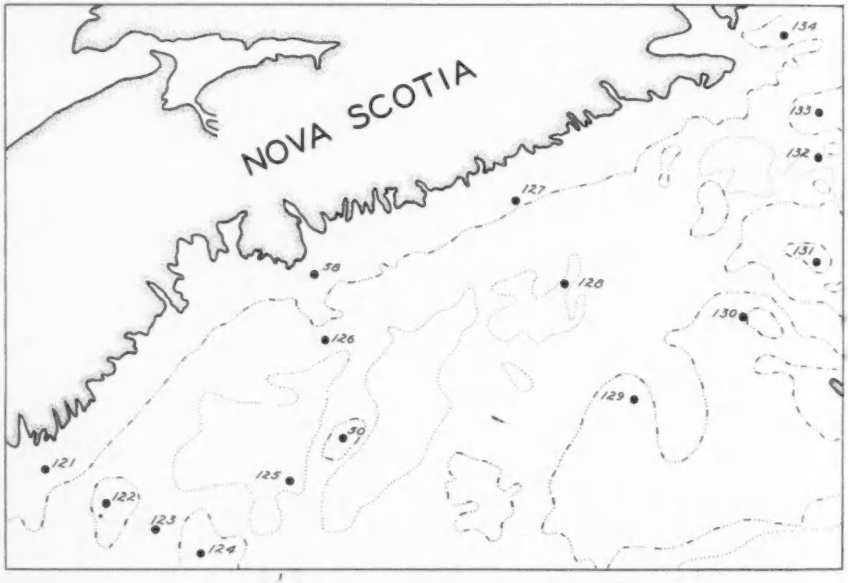

Figure 1. Locations of hydrographic stations.

121 to 124, 58 to 50, 127 to 129, and 134 to 131 are approximately at right angles to, while the lower two sections 124 to 50 and 129 to 131 are roughly parallel to, the south coast of Nova Scotia. Of the upper four sections, which extend outward from the coast, section 134 to 131 at the extreme east is peculiar in having no water temperatures higher than 2°C. This peculiarity is made possible by the comparatively shallow area that separates that section from that next to the west (127 to 129) and prevents interchange of water at depths below 50 m. In general there is an increase in temperature from the surface (minimum of −0.5° at stations 122 and 123) to the bottom (maximum of 7.9° at stations 128 and 125 in depths of 190 and 200 m. respectively). Where this order is reversed (sections

58 to 50 and 127 to 129 between 25 and 75 m.), the condition is known to be only temporary, before true winter conditions are reached. Temperature stratification tends to be less inshore, in part owing to mechanical mixing and in part owing to

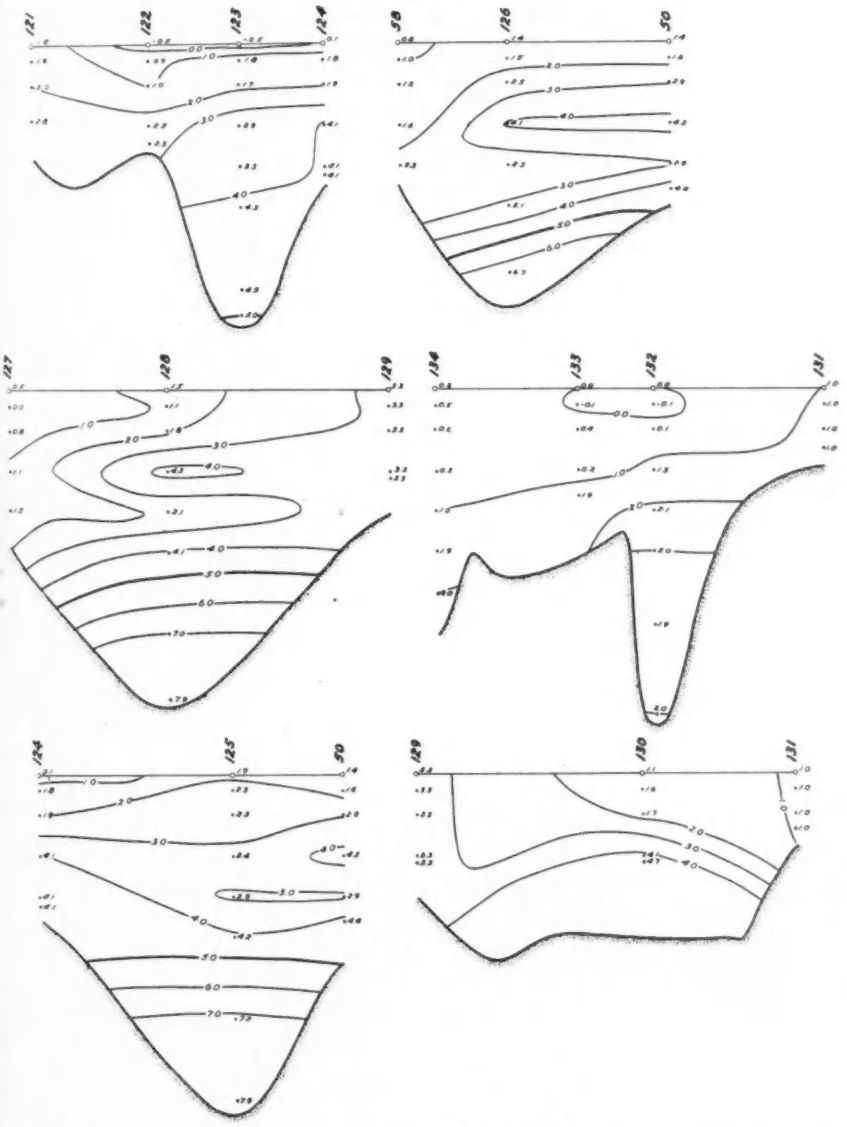

FIGURE 2. Sectional distribution of temperature for January 1938. Observations at 0, 10, 25, 50, etc. metres depth.

water transport from the east (Hachey 1938). The gradation in temperature from warm at the southwest to cold at the northeast will be apparent particularly in the two sections parallel to the coast (124 to 50 and 129 to 131) as between the deep station 125 and the shallow station 131.

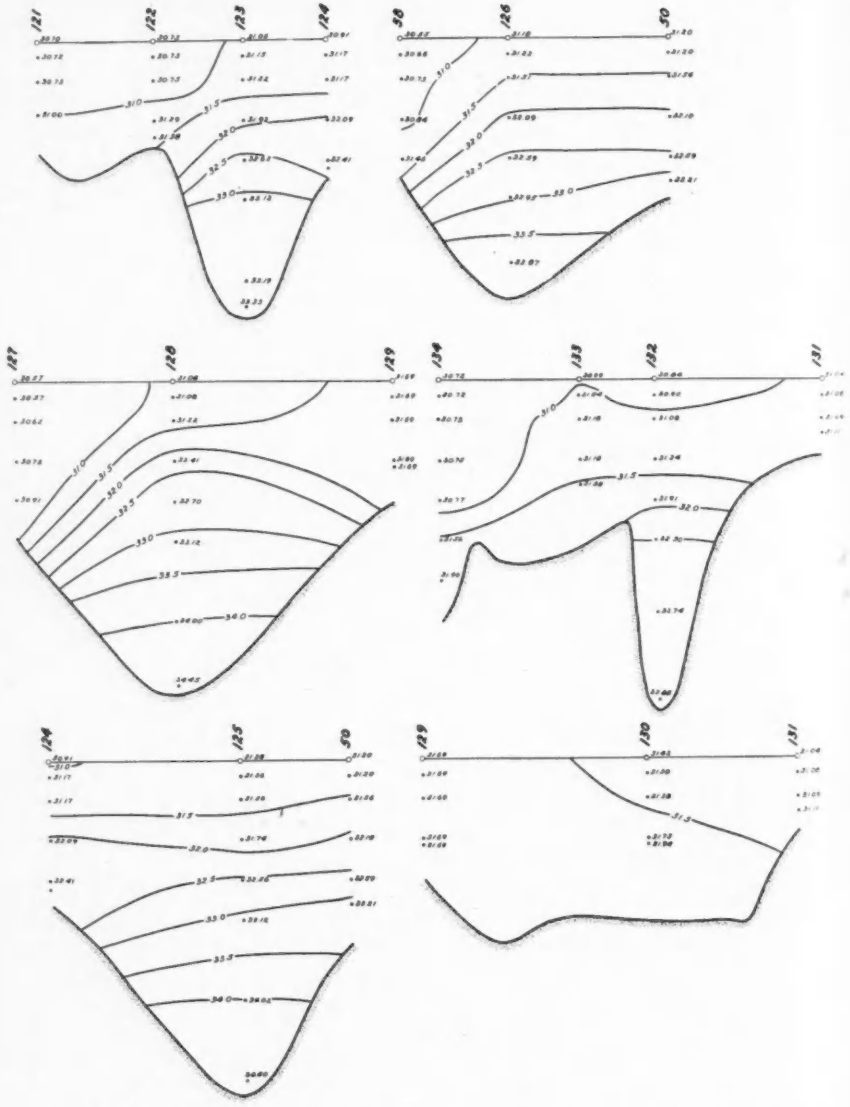

FIGURE 3. Sectional distribution of salinity for January 1938. Observations at 0, 10, 25, 50, etc. metres depth.

Salinity (fig. 3) increases with depth from a surface minimum of 30.55‰ (station 58) to a maximum of 34.45 at 190 m. (station 128). Waters of low salinity are against the coast. The lack of interchange of deep water between the two

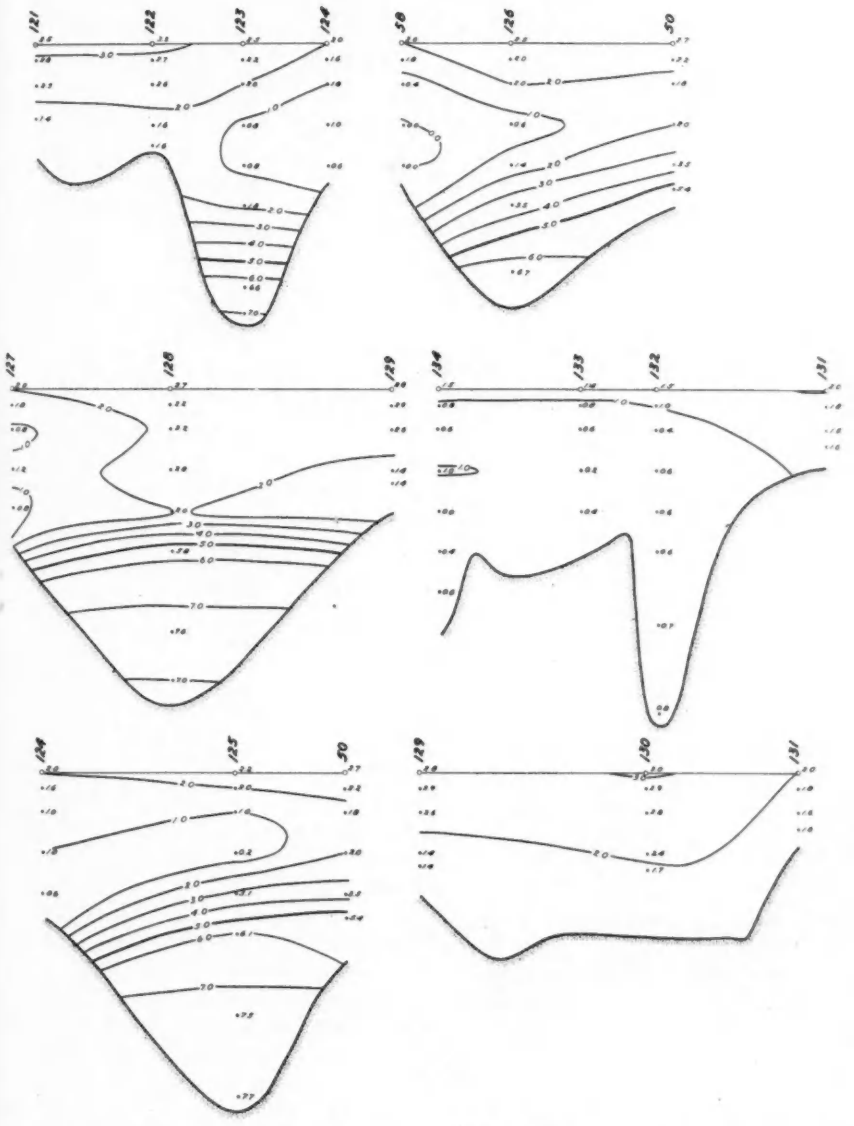

FIGURE 4. Sectional distribution of temperature for April-May 1938. Observations at 0, 10, 25, 50, etc. metres depth.

eastern sections (127 to 129 and 134 to 131) is shown by the differences between stations 128 and 132 below 50 m. (32.41 to 34.45 versus 31.24 to 32.88).

After the winter conditions just described for January, surface temperatures decreased to minimal levels, and by the time of the *spring* observations shown

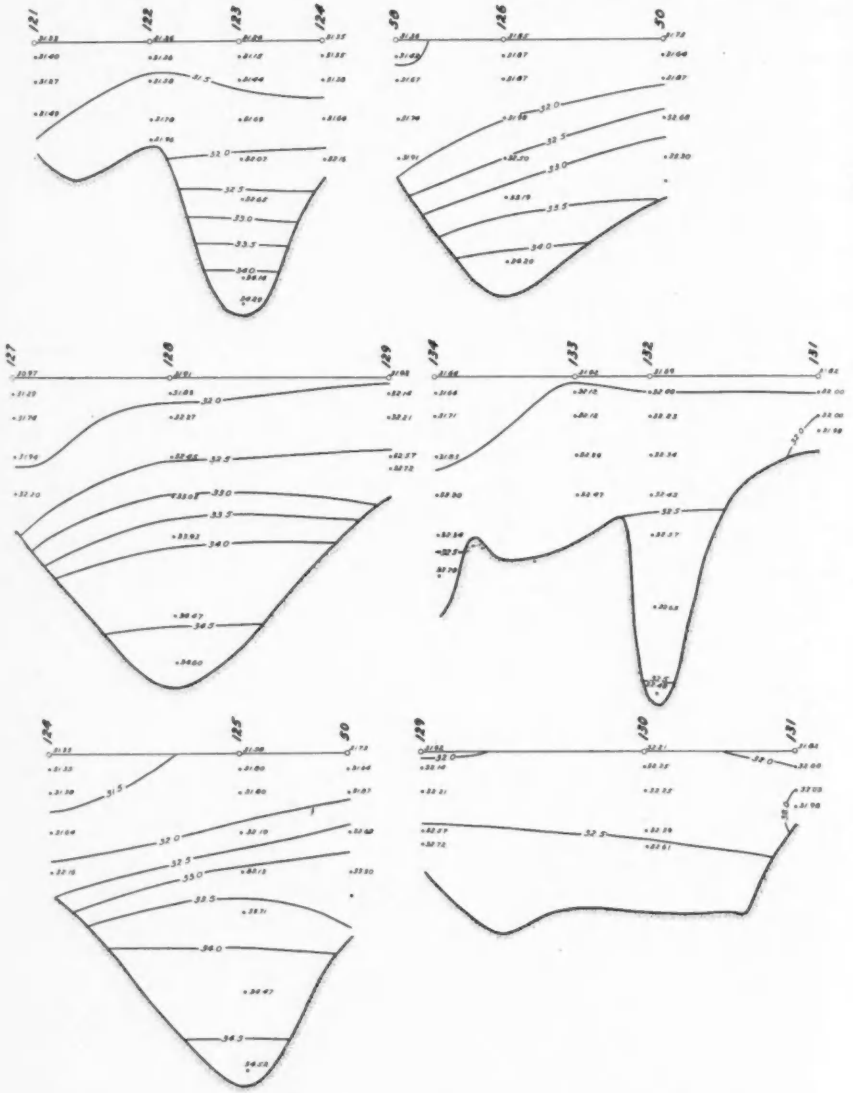

FIGURE 5. Sectional distribution of salinity for April-May 1938. Observations at 0, 10, 25, 50, etc. metres depth.

for April-May of 1938 in figure 4, there had already been some vernal warming, the lowest surface temperature (1.4°C.) being at station 133. In most sections temperatures have risen above 2.0° even as deep as 75 m. This results in an intermediate "cold water layer" between upper and lower warmer waters, but in the easternmost sections (134 to 131 and 129 to 131) temperatures are comparatively uniform and lower than in January. Water movements are quite prominent during the winter months (Hachey 1938, 1940), hence lowering of the temperature is probably due more to water replacements than to surface cooling. Waters warmer by 2° have entered section 121 to 124 near the bottom between January and April. In this interval, too, the winter isotherm of 2° (warmer water below) has disappeared from the eastern sections and has gone down elsewhere to 50 m. or deeper. As the 5° isotherm has suffered little displacement (except upwards in 121 to 124 by 50 m.), temperature stratification between 75 and 100 m. has become more pronounced.

There has been a general increase in salinity between January and April, as seen on comparing figure 3 with figure 5, and this is made particularly evident near the surface by the almost complete disappearance of salinities less than $31^0/_{00}$.

In *summer* (fig. 6 for August, 1938), three important water layers may usually be readily differentiated: (1) an upper layer warmer than 5°, as warm as 20.1°, from 20 m. (station 121) to 55 m. (station 130) thick; (2) an intermediate layer colder than 5°, extending from 20 m. (station 121) and 55 m. (station 130) depth to 85 m. (station 125) and 125 m. (between 127 and 128), but the corresponding water extends to the bottom in sections 134 to 131 and 129 to 131; and (3) a bottom layer from 5° to 8° in temperature (absent in the eastern sections), whose thickness depends chiefly upon bottom topography. The principal change from April to August has been the development of the upper layer of comparatively warm water.

The summer salinities (fig. 7) are in all sections partially less than $31^0/_{00}$ near the surface, a decrease from spring. This is accompanied by slight increases in bottom salinity, with a highest recorded value of $34.69^0/_{00}$, which can mean only an ingression of offshore waters. This is the usual condition which suggests that ingression near the bottom of water from offshore is more effective in summer.

Since salinity is a more reliable characteristic than temperature for defining the upper layer of water, which becomes so cold in winter and so warm in summer, it may be used to differentiate the three layers mentioned above. As defined by temperature, the upper layer has a salinity at different stations ranging from less than $32.5^0/_{00}$ (station 126) to less than $32.1^0/_{00}$ (station 123), the intermediate layer has a salinity with these at low levels to high levels ranging from $33.55^0/_{00}$ (station 50) to $33.80^0/_{00}$ (station 126), and the bottom layer has still higher salinities. The three layers may be redefined as follows: (*a*) an upper layer with salinity less than $32.0^0/_{00}$; (*b*) an intermediate layer with salinity between 32.0 and $33.5^0/_{00}$; and (*c*) a bottom layer with salinity greater than $33.5^0/_{00}$. So defined, their thicknesses in the various seasons, as shown in figures 3, 5 and 7, varied in 1938, depending upon the location for the upper layer between 0 and 115 m. in winter, between 0 and 85 m. in spring, and between 20 and 60 m. in

summer; for the intermediate layer they were in the southwesterly portion of the shelf between 30 and 85 m. in winter, between 40 and 85 m. in spring, and between 55 and 90 m. in summer, and for the bottom layer (absent to the northeast) they were limited by the bottom configuration.

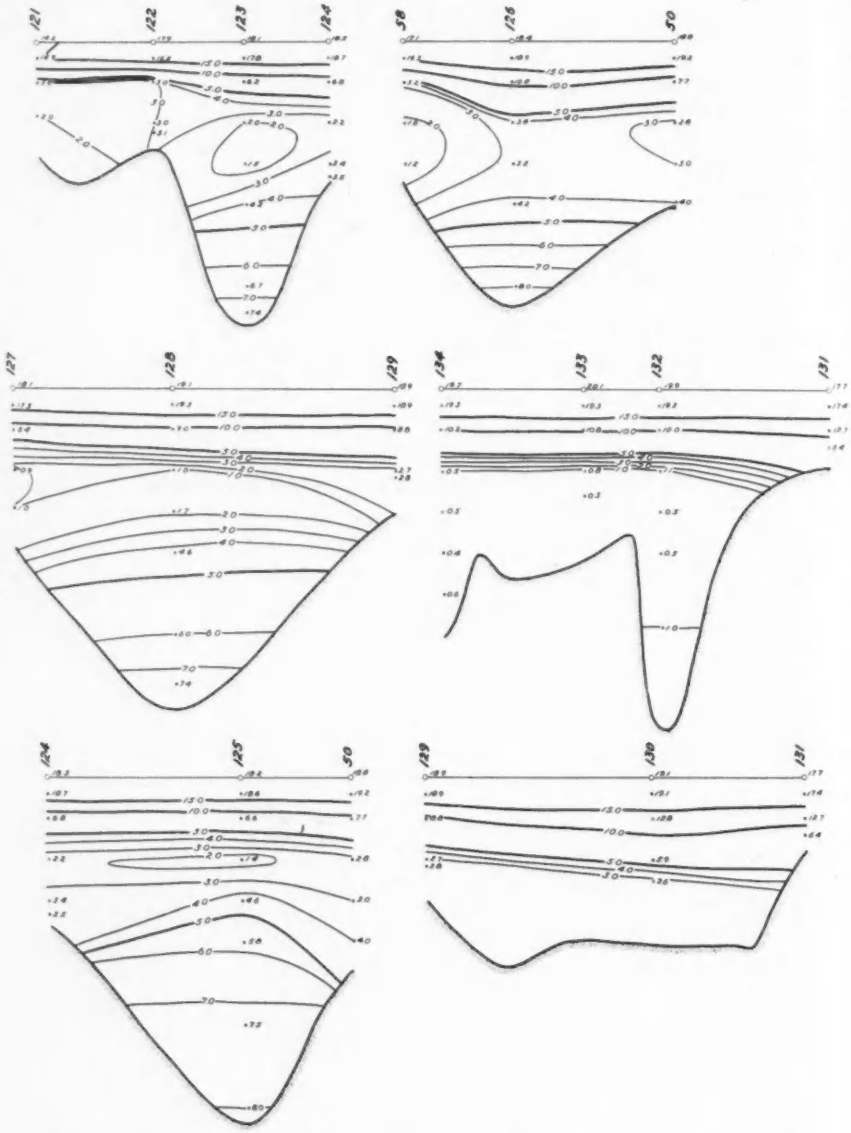

FIGURE 6. Sectional distribution of temperature for August 1938. Observations at 0, 10, 25, 50, etc. metres depth.

A former classification of Canadian Atlantic waters (Bjerkan 1919), based on spring and summer cruises over an extended area, defines "coastal", "intermediate", "bank", "slope", and "Atlantic" water. The "upper layer" in the present classification comprises "coastal" and "intermediate" water, the "inter-

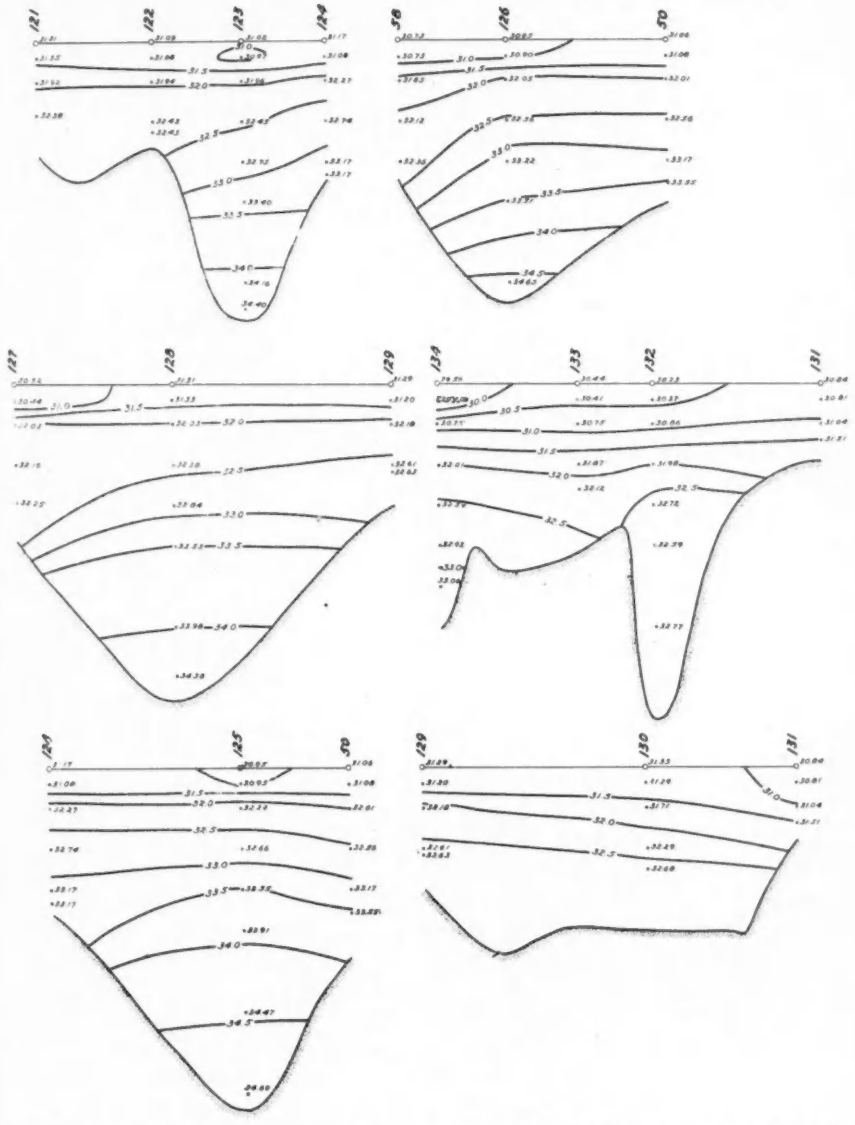

FIGURE 7. Sectional distribution of salinity for August 1938. Observations at 0, 10, 25, 50, etc. metres depth.

mediate layer" corresponds with "bank water", and the "bottom layer" with "slope water". Bjerkan's classification was seemingly suggested by the horizontal distribution of salinity in the surface waters, during spring and summer, from the coast outwards, and it is obvious that "coastal" refers to the surface waters holding close to the coast in spring and summer, "bank" to those surface waters found over the fishing banks, while "intermediate" refers to those surface waters found in spring and summer between "coastal" and "bank" waters. The term "slope" refers to those waters found at the edge of the continental shelf, while "Atlantic" refers to true ocean waters. While the terms were probably suggested by the horizontal distribution in spring and summer, the distribution in depth was taken into consideration by Bjerkan. In dealing with the characteristics of the Scotian shelf only, the particular interest would seem to lie in the vertical distribution of the waters rather than in the horizontal, as the so-called "intermediate layer" is the outstanding feature of the area. Further than this Bjerkan's "Atlantic" water is seldom, if ever, found in the area, and water having the characteristics of "coastal" is entirely absent during the winter season. A reasonable modification of Bjerkan's terminology would be possibly the application of the term "coastal" to include also the "intermediate". In any event, in dealing with the seasonal changes of the waters of the Scotian shelf, the terms "coastal" and "intermediate" become unwieldly, and as the greater interest is seen in the vertical distribution, the waters are treated herein as consisting of three different layers which are readily related to the classification outlined by Bjerkan.

AS SHOWN HORIZONTALLY

In *winter* (fig. 8 for January, 1938), surface waters with temperatures less than 1°C. (total range −0.1 to 3.3°) are found in quantity to the northeast, and in small amount to the southwest. The warmest water (about 3.0°) is offshore at station 129. At 50 m. depth, with total range from 0.32 to 4.29°, the warmer water (over 4°) is offshore and the colder water inshore and at the north, where it is less than 1°. At the bottom, ignoring depth, there is great variation (1.02 to 7.92°), with temperatures less than 3° confined to the coast and the extreme east and those above 5.0° to the greater depths.

Surface salinities less than 31‰ (total range 30.55 to 31.69‰) are correlated with temperatures less than 1°, and those between 31.0 and 31.5‰ with temperatures between 1 and 3°. At 50 m. depth, with a range from 30.73 to 32.41‰, there is a similar correspondence between 31.5‰ and 30, and isohalines, like isotherms, tend to run parallel to the coast. At the bottom with range from 31.00 to 34.45‰, salinities less than 33‰ are confined to the coast, to the shallower areas offshore and to the eastern portion of the area.

In *spring* (fig. 9 for April-May 1938) surface temperatures ranging from 1.4 to 3.5° reflect vernal warming, with the colder water at the northeast. At 50 m. the temperatures (−0.2 to 2.82°) are on the whole lower than in January, reflecting movement of colder water from the northeast in winter (Hachey 1938) and the warmer water (above 2°) is chiefly in the centre of the area. At the bottom there is little change from the January condition except a marked lowering of temperature at the east.

Surface salinities (31.26 to 32.21‰) are lower at the extreme southwest, and are in general about 0.5‰ higher than in January. These conditions hold at 50 m. depth with a higher range (31.64 to 32.68‰), and the general increase holds also for the bottom with range from 31.91 to 34.60‰.

In *summer* (fig. 10 for August 1938) surface temperatures with a range from

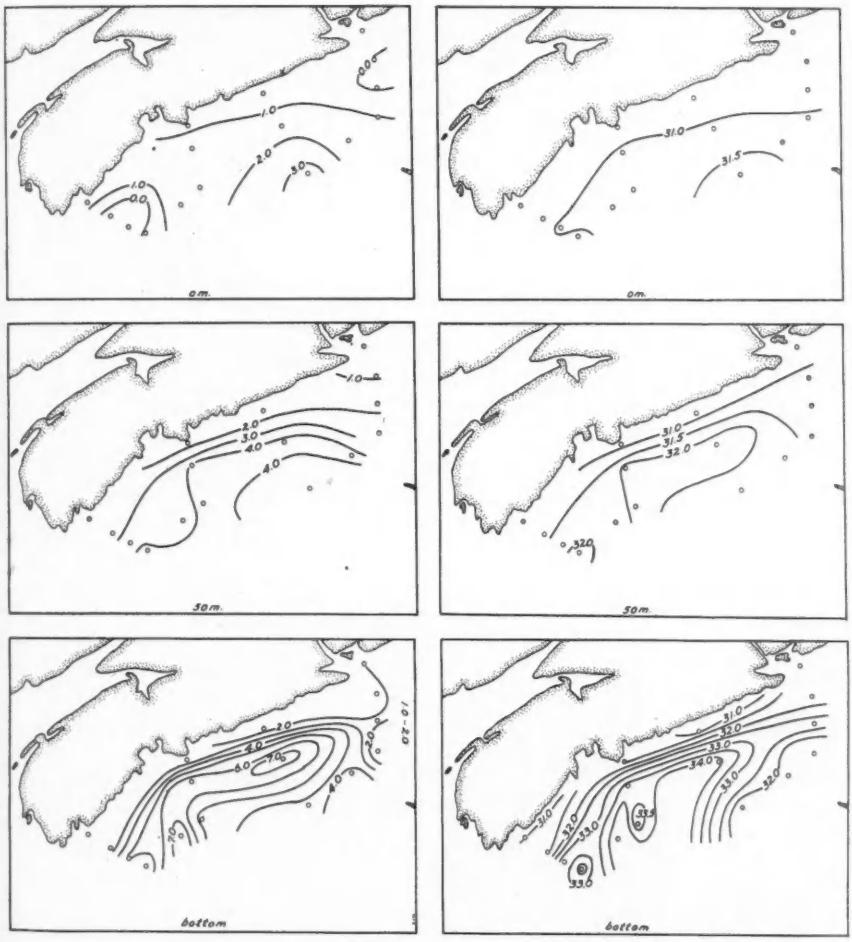

FIGURE 8. Horizontal distribution of temperature and salinity in January 1938.

14.2 to 20.1° are lowest inshore at the southwest (doubtless due to upwelling) and highest at the extreme northeast. At 50 m., with range from 0.48 to 5.85°, the lowest temperatures are inshore and the highest offshore at the northeast, and there has been a rise since April-May. At the bottom (range, 0.49 to 8.02°) there is the same change for the shallower eastern banks (even from 1.61 in April-May

to 6.0° in August), and water above 7° has penetrated the deeper part of the area.

Surface salinities (29.56 to 31.33‰) are approximately 1‰ lower than in spring, but at 50 m. salinities (31.87 to 32.74‰) are slightly lower, and at the bottom with range from 31.51 to 34.69‰ they are little changed except that deep penetration of water with salinity above 34‰ has occurred.

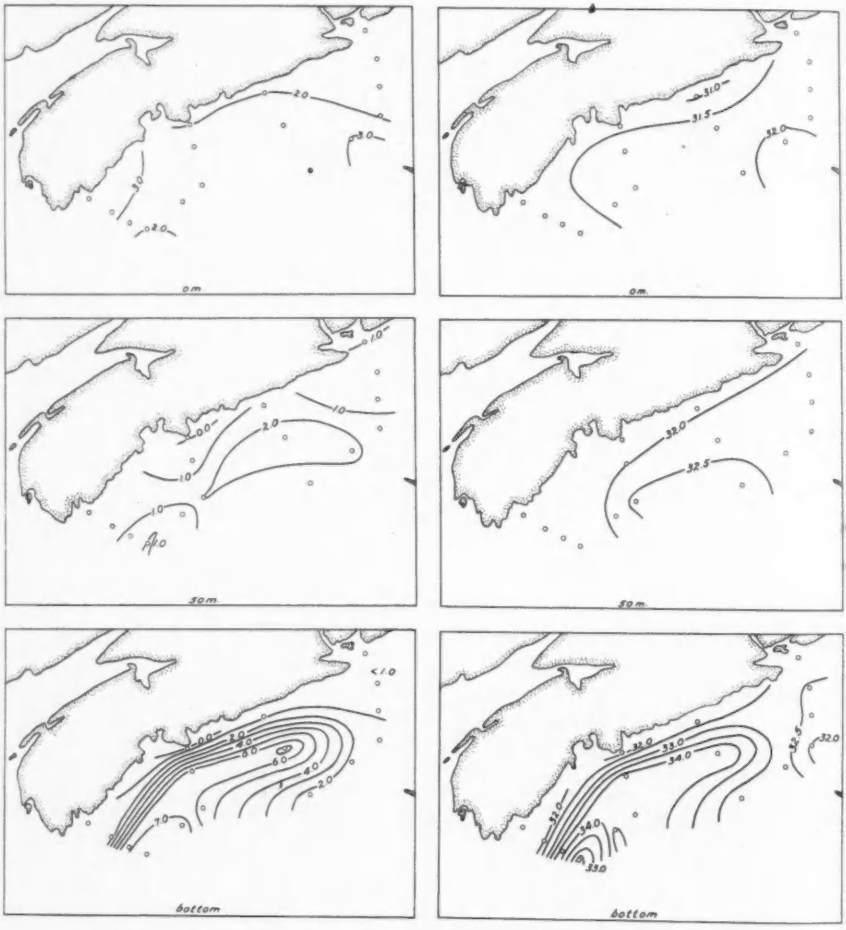

FIGURE 9. Horizontal distribution of temperature and salinity in April-May 1938.

CHANGES FROM YEAR TO YEAR

While the 1938 observations furnish a more or less general picture of the water conditions, annual differences have been observed, which, although comparatively small, may have far-reaching influences. For 1935 it was quite obvious that colder waters from the northeast exerted such a profound influence on the

waters of the area throughout the greatest part of the year that it was termed the "cold water year". In contrast it was observed that in 1934 the transport of water from the northeast was smaller than usual, and the influence of the warmer offshore waters was so great that it was termed the "warm water year". These two were the extreme years from 1934 to 1938.

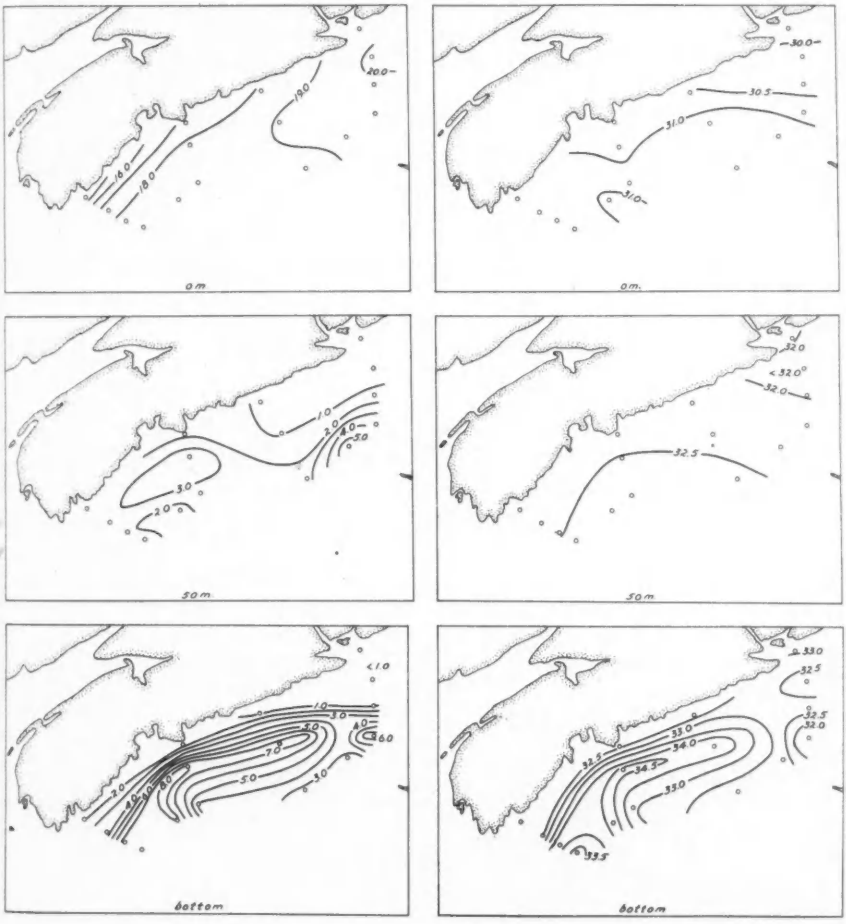

FIGURE 10. Horizontal distribution of temperature and salinity in August 1938.

Surface temperatures (fig. 11) were for May in general higher than 4° in 1934 and lower than 4° in 1935. The isotherms tended to be parallel to the coast in 1934, indicating movement of warm water inward, and to be more or less at right angles to the coast in 1935, indicating movement of cold water from the northeast. For August, the offshore origin of the warm water in 1934 was even more

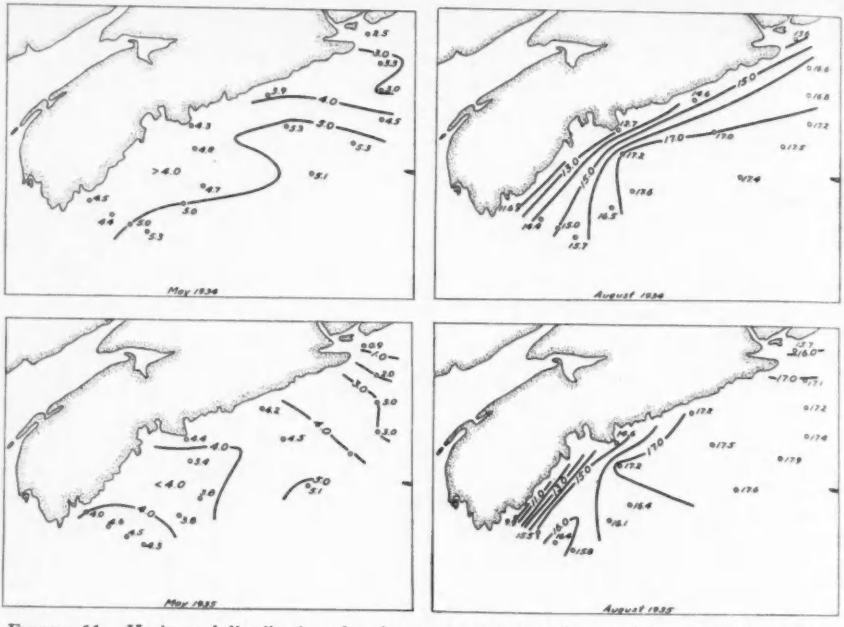

FIGURE 11. Horizontal distribution of surface temperatures in May and August 1934 and 1935.

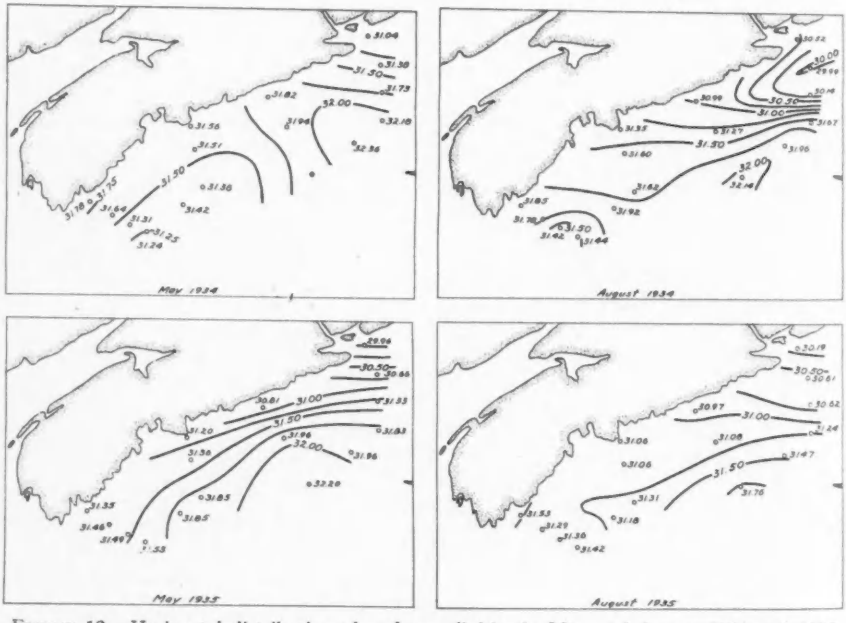

FIGURE 12. Horizontal distribution of surface salinities in May and August 1934 and 1935.

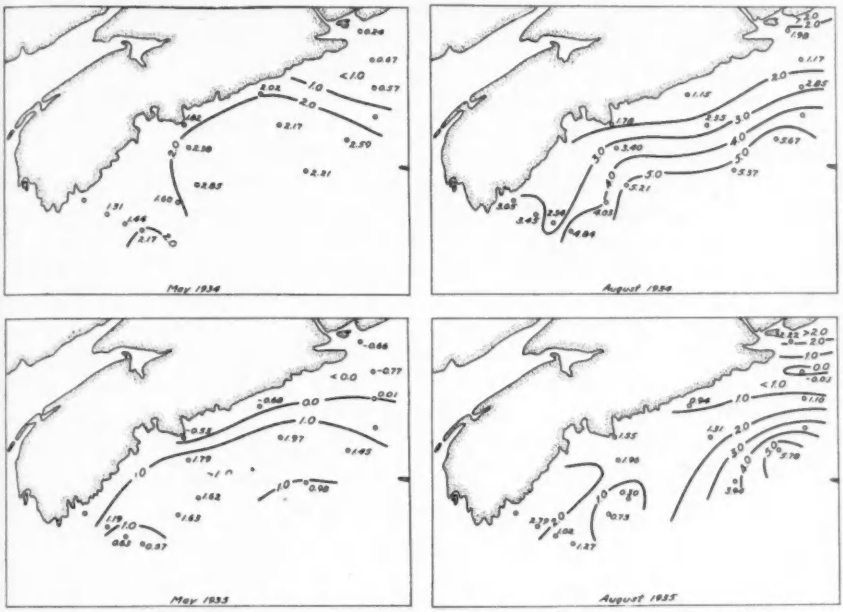

FIGURE 13. Horizontal distribution of temperature at 50 m. in May and August 1934 and 1935.

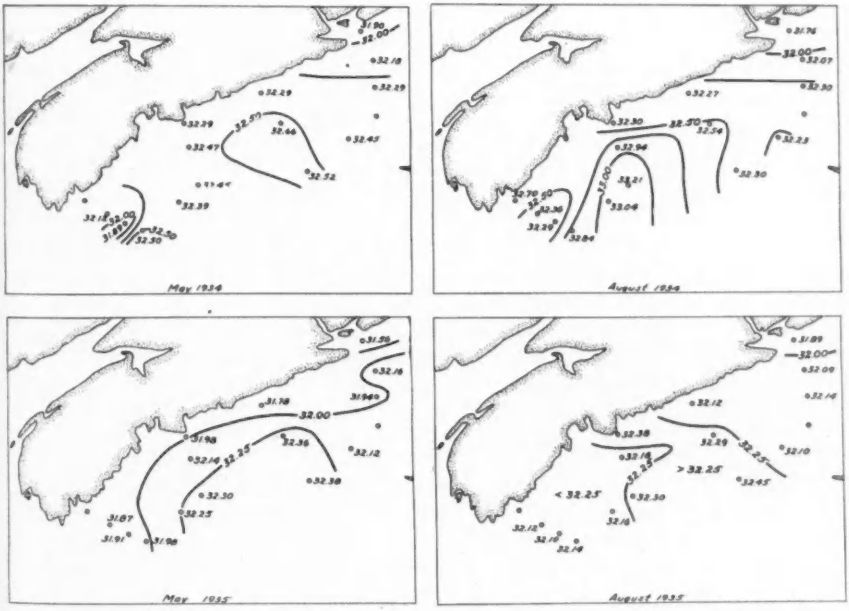

FIGURE 14. Horizontal distribution of salinity at 50 m. in May and August 1934 and 1935.

evident from isotherms paralleling the coast, but in 1935, although there was little of such paralleling, the lowest temperatures were at the extreme southwest where upwelling was most marked, and water above 17° seemed to originate offshore to the northeast, which corresponds with bottom configuration (Hachey 1937a).

Surface salinities (fig. 12) confirm this picture in more striking fashion. For May in 1934 water above 31.5‰ was well inshore along almost the whole coast, while in 1935 there was a wide coastal band of water below 31.5‰. Similarly for August, in 1934 there was considerable water above 31.5‰ and close inshore at the southwest, while in 1935 such water was observed only at the outermost station.

Temperatures at 50 m. depth (fig. 13) for May were in 1934 above 2° over a large portion of the area and were nowhere below 0°, while in 1935 they were nowhere as high as 2° and there was a band of water less than 0° extending along the coast from the northeast. For August, the temperatures averaged about 3° in 1934 and 2° in 1935. In 1934 over half the area had temperatures above 3°, but in 1935 only a small part had such.

Salinities at 50 m. depth (fig. 14) for May were higher in 1934 than in 1935, water above 32‰ being close inshore at least centrally in 1934 but nowhere inshore in 1935. Similarly for August there was considerable water above 32.5‰ in 1934, but none in 1935.

INSHORE VERSUS OFFSHORE WATERS

Inshore Waters

It is readily seen from the data for station 60 for depths of 0, 50 and 100 m. (figs. 15 and 16) that there is generally a comparatively high salinity stratification, but a generally uniform temperature from 50 to 100 m. except late in the year.

TEMPERATURE CHANGES

The extremes are 19.8° (September 6, 1932) and −1.0° (January 19, 1935). There were higher values at the surface in 1932 and 1933 than in 1934 and 1935. At 50 m. depth, temperatures are generally less than 5°, but in late summer in some years may increase sharply and persist, which phenomenon has been dealt with previously (Hachey 1935b). Conditions at 100 m. tend to follow those at 50 m., but are less extreme.

For a short period in early winter occurs the annual overturn brought about by surface chilling, which causes vertical circulation and a uniform temperature to considerable depths. This is a general coastal phenomenon in the Canadian Atlantic, but it should be appreciated that conditions at station 60 are determined by water movements from the east which bring the results of surface chilling elsewhere (Hachey 1938). Further cooling throughout the winter tends to continue the vertical circulation and the uniform temperature as shown best by observations for the winter of 1934-1935.

The annual cycle in surface temperature is from a winter minimum, usually in February, to a late summer maximum, usually in September, and back to the winter minimum. This cycle is somewhat disturbed by shoreward movements in late autumn, and it is also interrupted by any removal of the surface water accompanied by upwelling of colder water. At 50 m. depth also, the minimum is in February, but the manner of the rise to the maximum varies considerably from year to year. In 1932 and 1933 the rise was gradual until late August and then abrupt to a September or October maximum. In 1934 and also in 1935 the rise was rather gradual to a December maximum. The abrupt rises in late summer are the result of the replacement process in inshore waters at times of

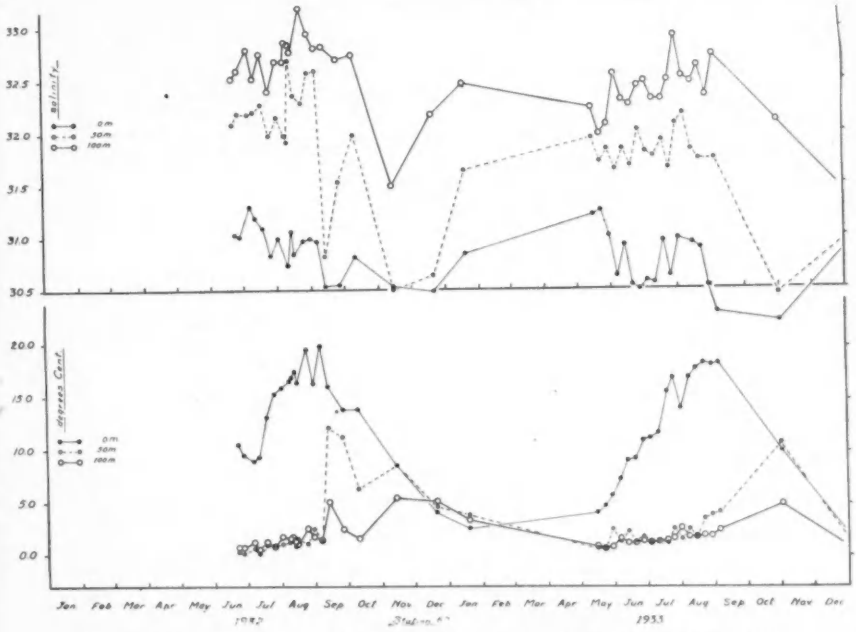

FIGURE 15. Temperature and salinity variations at station 60 for 1932 and 1933.

steep atmospheric gradients over the neighbouring ocean (Hachey 1935b). At 100 m. depth this replacement will also disturb the regularity of the cycle, which shows a minimum in late winter, spring or summer, and a maximum in any month of the late autumn or early winter.

SALINITY CHANGES

The minimum surface salinity (as low as 30.17‰) is during the autumn (1932, 1933 and 1934), but in 1935 comparatively low salinities occur in both spring and autumn. Surface salinities were higher in 1934 than in other years (maximum for the period, 31.69‰ in December, 1934). At 50 m. depth abrupt changes in salinity occur, as particularly in 1932 and 1933 during autumn, and

they are another phase of the phenomenon recognized by the abrupt temperature changes previously mentioned. At 50 m. minimum salinities were in late autumn in 1932 and 1933, but in early winter at the annual overturn in 1934 and 1935.

As will be seen for 1933 and 1934, the annual overturn in some years is effective to depths of at least 100 m. Apparently it was not so in 1932-1933. At 100 m. depth salinities show the largest annual variation and, as at the surface, they were somewhat higher in 1934 than in other years.

Offshore Waters

The data for the selected stations (125 and 128) are plotted in figure 17 to show the vertical distribution of temperature and salinity at different times in the year.

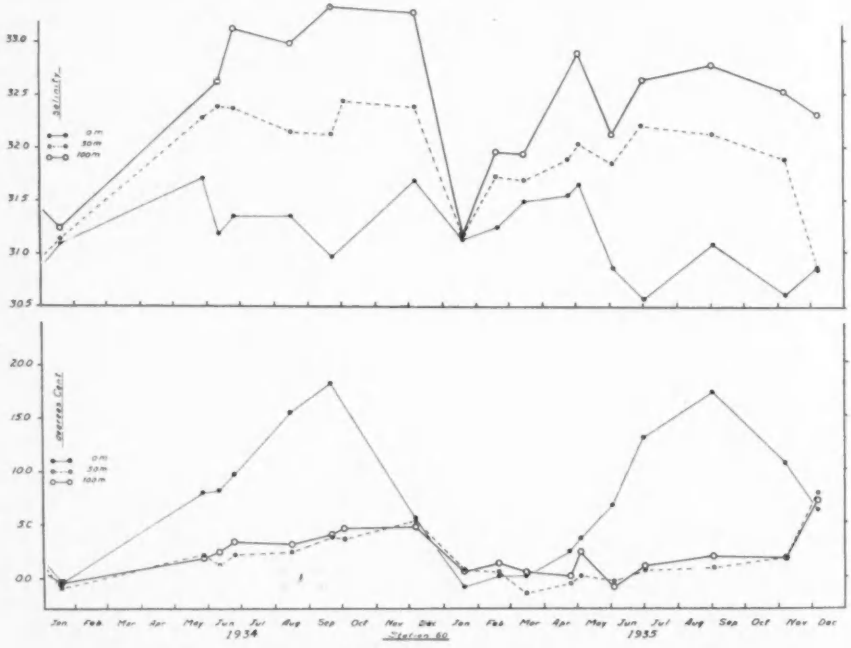

FIGURE 16. Temperature and salinity variations at station 60 for 1934 and 1935.

TEMPERATURE CHANGES

It will be seen that at station 125 from April 28 to May 31 the temperatures of the upper 25 m. increased approximately 3°, and that the increase lessened gradually from 25 to 75 m., which is to be ascribed to vernal warming. The increase of more than 1° at 150 m, depth indicates water replacement. Similarly by June 17 vernal warming had increased the upper 10 m. 5° more, and was effective at least down to 25 m. Increases of about 2.5° between 75 and 150 m. indicate large scale water replacement. By August 22, there was a further increase

for the upper 25 m. of more than 6°, and of approximately 1° at all depths below 50 m. From the summer condition of August to the winter condition of February, surface cooling was the main cause to bring about uniformity to considerable depths. However, we should not overlook the action of horizontal movement in bringing the results of surface cooling in far distant areas. It has been demonstrated (Hachey 1938) that "winter chilling in situ" is negligible compared with

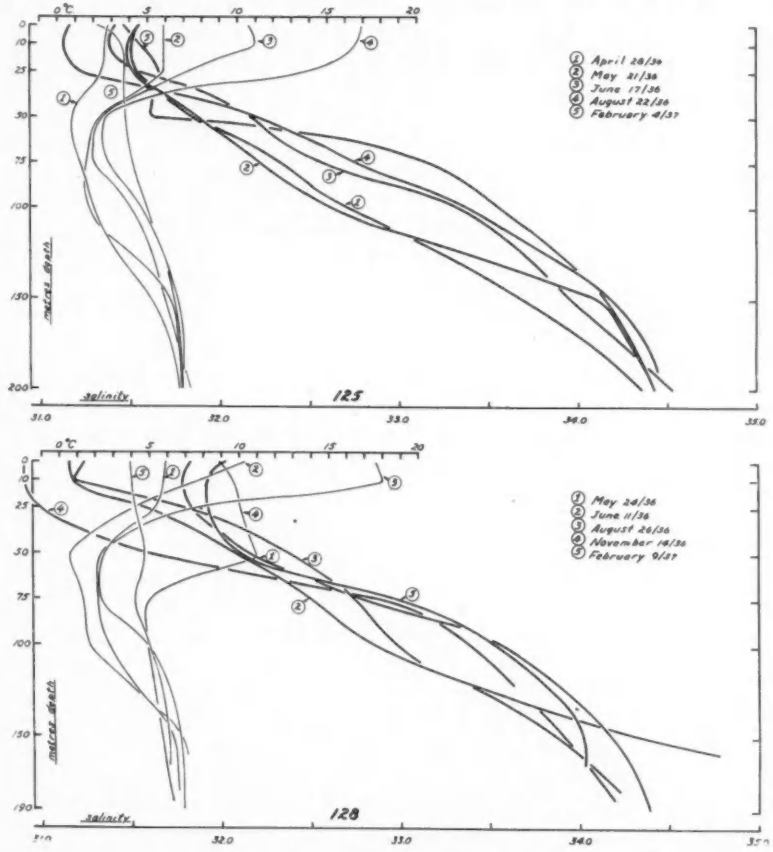

FIGURE 17. Seasonal variation in temperature-depth (light lines) and salinity-depth (heavy lines) relationships at stations 125 and 128.

water movement from the northeast in producing the cold water layer of the Scotian shelf. As a result of the processes operating between August 1936 and February 1937, the temperature of the upper 50 m. decreased approximately 13° and that of the lower 50 m. increased approximately 1°.

At station 128 observations were made in November, as well as in August and February. These show that by November surface chilling had been effective

through vertical circulation to depths of at least 50 m., and by February probably to a depth of 75 m.

SALINITY CHANGES

Below 50 m. depth at station 125 the salinities show in general a progressive increase from April and May to February, with less than $1^0/_{00}$ change. Below 150 m. the highest salinity was $34.54^0/_{00}$ at 200 m. in June, but the highest salinities of the water as a whole would seem to have been reached in August. From April and May to June and August the salinities of the upper 25 m. decrease, but at 50 m. they increase. By February there is quite uniform salinity in the upper 50 m.

At station 128, observations in November show the lowest salinities of the year for the upper 50 m. occurring at that time. That waters of salinity less than $32^0/_{00}$ are involved in the outflow from the gulf of St. Lawrence has been demonstrated by the investigations of the Canadian Fisheries Expedition of 1914-1915 (Bjerkan 1919). This outflow, apart from waters of limited extent affected by river freshets, seems to reach its lowest salinity in late summer and autumn, and, hence, if it reaches the Scotian shelf, it will give lower surface salinities late in the year.

SUMMARY

The year 1938 is taken to show conditions in the water of the Scotian shelf at various seasons, and 1934 and 1935 are taken to show differences between years. The comparatively shallow eastern part of the area (east of Sable island bank) differs from the rest chiefly because the bottom configuration prevents direct interchange of water below 50 m. depth, but also to some extent because the shallowness offers resistance to the general tendency of the surface waters to move from east to west.

In winter (January): temperatures at the surface are as low as -0.5°C. (may become lower later in the winter), and at the bottom as high as 7.9°; salinities at the surface are as low as $30.55^0/_{00}$ and at the bottom as high as $34.45^0/_{00}$; east of Sable island bank at all depths low temperatures (less than 2°) and low salinities (less than $32.9^0/_{00}$) prevail.

In spring (April-May): vernal warming is shown by a warm surface layer extending even to 75 m. depth and distinct from the subjacent "intermediate cold water layer"; penetration of warmer water at the bottom in certain areas is shown by temperatures as much as 2° higher than in January.

In summer (August): there is full development of the warm "upper layer" and complete isolation of the cold "intermediate layer".

Inshore waters have temperatures at the surface, ranging from -1.0 to 19.8°, and at 50 m. as low as -1.6°. The winter minimum generally occurs in February and the summer maximum usually in September. Generally the salinity is at a maximum in the spring and at a minimum in late summer. At 50 and 100 m. depth, maximum salinities are during the summer, and minimum in late summer and autumn. The annual cycle is disturbed somewhat by extensive shoreward

movements of surface water particularly in the latter part of the summer, and also by upwelling.

The three main layers have the following characteristics:

	Thickness (m.)	Temperature (°C.)	Salinity (‰)
"Upper" ..... Spring ..	0–85		
"Upper" ..... Summer	20–60	>5	<32.0
"Upper" ..... Winter ..	0–115	<5	
"Intermediate" Spring ..	40–85		
"Intermediate" Summer	55–90	<5 (generally)	32.0–33.5
"Intermediate" Winter ..	30–85		
"Bottom"	Limited by bottom configuration	>5 (generally)	>33.5

Offshore waters have minimum temperatures at the surface (as low as 2°) in January or February, and maximum temperatures as high as 20°. At 50 m. the minimum temperature observed (0.74°) was in late April and the maximum (3.78°) in the following February.

At 200 m. depth the minimum (6.68°) was in April and the maximum (7.34°) in June. Winter chilling is effective through vertical circulation at least to a depth of 50 m. by November and even to 75 m. by February. Salinites are highest at the surface in late winter or early spring and lowest in November, but at some depth (below 50 m.) they are highest in February and lowest in May or June.

REFERENCES

BJERKAN, PAUL. *Can. Dept. Naval Serv., Rep. Canad. Fish. Exped. 1914-15*, 309-403, 1919.

HACHEY, H. B. *Biol. Bd. Can., Prog. Rep. Atl.* **11**, 6-9, 1934.

Biol. Bd. Can., Prog. Rep. Atl. **16**, 3-6, 1935a.

J. Biol. Bd. Can., **1** (4), 227-237, 1935b.

Trans. Amer. Fish Soc., **66**, 237-241, 1937a.

Proc. N. S. Inst. Sci., **19**, (3) 264-276, 1937b.

Trans. Roy. Soc. Can., 3rd ser., **32** (3), 29-42, 1938.

LEIM, A. H., AND H. B. HACHEY. *Trans. Amer. Fish. Soc.*, **65**, 279-283, 1935.

Surface non-tidal currents in the approaches to Juan de Fuca strait

By John P. Tully
Pacific Biological Station

(*Received for publication June 30, 1941*)

ABSTRACT

The nature of the surface non-tidal circulation in the sea in the approaches to Juan de Fuca strait, latitude 48°30′N., longitude 125°00′W., is interpreted from stream line diagrams, four of which are reproduced. It is shown that the system represents a balance between a wake stream flow from Juan de Fuca strait, which is directly related to the volume of land drainage, and the independent wind-driven currents, which are due to one of the two prevailing coastwise winds in the area.

INTRODUCTION

The sea current configurations in the approaches to Juan de Fuca strait have been the subject of recent intensive investigations. The character and variations of the currents have proved to be of unusual interest because the current field represents a balance between the coastal wind-driven currents and land drainage discharge from the strait.

The area considered is centred around latitude 48°30′N. and longitude 125°00′W., as shown in the small square on the illustrative chart (figure 1).

Previously, Marmer (1926) made a series of surface current observations at Swiftsure lightvessel (48°35′N., 125°00′W.). His measurements were made with an adaptation of the *chip log* consisting of a long pole, which floated upright in the water, to which was fastened a long light line. The pole was allowed to drift away from the anchored lightship while the amount of line run out, the time, and direction of drift were observed. The resulting measurements of total current were analysed for harmonic components attributable to tide and for components variable with the wind, while the residue was regarded as land drainage or hydraulic current.

While these observations have the virtue of being absolute measurements of total current, they are limited to the surface current at one point and cannot illustrate the character or variations of the current system in the area. In order to overcome these limitations, recourse was had to dynamical methods based on the Bjerknes theorem of pressure gradients.

Bjerknes' theorem is a mathematical induction showing that, if there is a pressure difference in two vertical columns observed in a fluid medium on the earth's surface, then at equilibrium there is a current flowing, whose component normal to the plane joining the two observed columns is proportional to the pressure difference, the greater pressure being to the left of the current. It follows

J. Fish. Res. Bd. Can. 5 (4) 1942
Printed in Canada

that the currents must flow along the paths of equal pressure (stream lines) and if a current is imposed in such a medium, a pressure adjustment must take place, which at equilibrium will represent the current force.

An analysis based on this theorem describes the current field at any depth between a number of observed columns, which may be so arranged as to show the path of the current by means of pressure contours (stream lines), and the velocity by the gradient across the path of flow. It is necessary to assume that the bottom water is motionless or has a negligible movement, that the current-producing forces and nature of the water masses involved are constant during the period of observation, and that the system is in a state of equilibrium. It is at once evident that the limiting conditions cannot be strictly fulfilled in any natural system, and consequently any conclusions must be regarded as approximations within these limits. However it has the advantage of permitting the description of the current field in any area which can be surveyed during approximately constant conditions.

In this series of surveys observations were made of the density of the water at suitable intervals of depth, and at the positions indicated by the black dots in figures 4, 5, 6, and 7. The position of the stream lines and the velocities of the current components were calculated with reference to the conditions at a base depth of 200 metres in figures 4 and 7, and to those at 150 metres depth in figures 5 and 6, by the standard methods (Smith 1926). Stations having less than the base depth were extended to this level by the method of Helland-Hansen (1934). Due regard was given to the limiting conditions, and all observations were made when the weather conditions had been established for several days and continued generally constant throughout the series, which was always completed within one week.

Parr (1938) has registered objections to the use of stream lines to represent the trajectory of flow and has suggested the employment of isentropic charts. In order to test the validity of the current diagrams obtained by the application of Bjerknes' theorem, isentropic charts were constructed by plotting the distribution of dissolved oxygen on an isopycnal layer near the surface, similar to the method outlined by Rossby (1937) for atmospheric isentropic analyses. Except for some minor instances, which in no way affect the present discussion, the flow as defined by both methods agreed entirely. Consequently in this instance the pressure diagrams may be regarded as a reasonably accurate representation of the equilibrium current system.

Causes of Currents

The currents in the area may be regarded as partly due to external forces, namely the tide, land drainage or hydraulic currents through Juan de Fuca strait, and wind or drift currents. These are the causative forces recognized by Marmer. However, since there are sources of water of varying density in the area, it follows that there must be differences of pressure and consequently a system of gradient currents which may be regarded as of internal origin.

Tide

Marmer showed that the tidal current was semi-daily in the area, reversing in Juan de Fuca strait, and rotary at Swiftsure lightvessel, which is eleven miles (18 km.) offshore. The tides at the latter position are assumed to be representative of those in the whole area included in this discussion.

Several surveys have been undertaken to determine the effect of the tide on the position of the stream lines, and it was found that the whole non-tidal current field rotates about an elliptical path with only minor distortion. It appears that tidal currents do not maintain their force and direction for sufficient time to

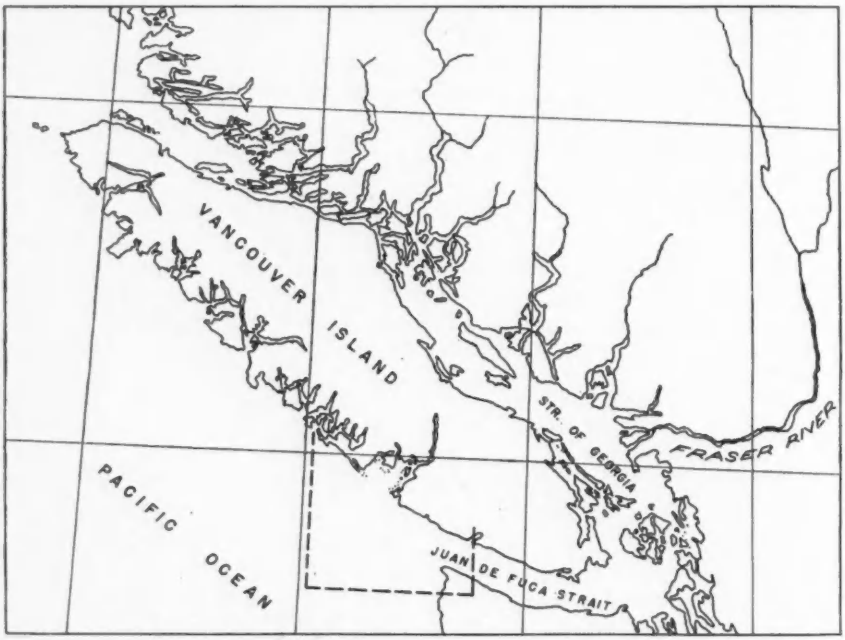

Figure 1. Pacific coast of Canada showing the area studied (inside the interrupted line), Vancouver island, Juan de Fuca strait, Georgia strait and the Fraser river.

attain an equilibrium and so build up a field of stream lines representing the flow. Consequently the purely tidal currents are not shown in the diagrams of stream flow.

RESULTS

Land Drainage

Juan de Fuca strait extends from the sea inland to Georgia strait (fig. 1). There are many rivers flowing into these straits, of which the Fraser river is the largest, contributing about seventy per cent of the total land drainage into the system. This fresh water moves seaward at the surface, creating a steady ebb

current superimposed on the reciprocal tidal currents, and the deep ocean waters enter Juan de Fuca straits at the bottom forming a counter current to the steady component of the surface flow. Owing to the presence of many narrow passages, and the large amount of tidal and drainage water passing through the system, the currents are very rapid (attaining velocities as high as five to ten knots) and turbulent. As a consequence, the fresh land-drainage waters become so thoroughly mixed with the deep ocean waters that the resultant density of the outflowing surface waters is as high, and at times higher, than the surface ocean waters near the coast. Although the character of the drainage waters is lost, the pressure of the seaward non-tidal flow at the surface is maintained by land drainage, and it is most convenient to assume that this flow varies as the discharge from the Fraser river (fig. 2).

Rossby (1938) and Spilhaus (1938) have discussed this type of circulation where the flow from an orifice enters a large rotating body of water. They showed

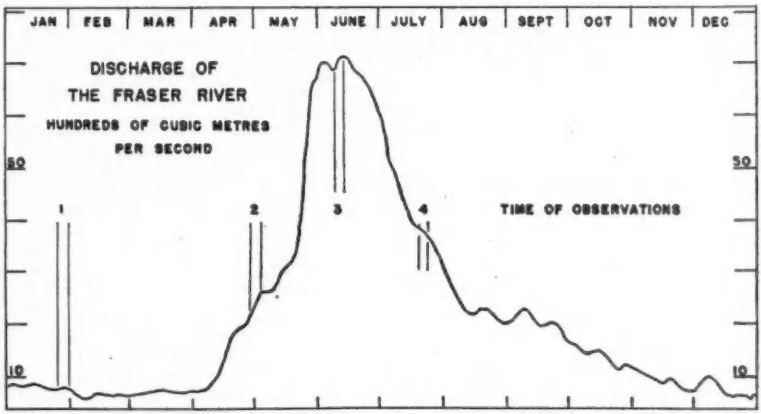

FIGURE 2. Daily discharge of the Fraser river during the year in which the current observations were made. The data are smoothed by sevens, and the "Time of observations" indicates by parallel vertical lines when the data for each of figures 4, 5, 6 and 7 were obtained.

that it is a necessary consequence in the northern hemisphere that the *wake stream* should veer to the right, that there should be a counter current along the left side of the wake stream from which water is absorbed, that water should be discharged from the right side of the stream in the form of eddies, and that the force of the stream is finally dissipated in these eddies. Rossby shows that the counter current is in fact a dependent stream having the same characteristics of transporting water from left to right as the wake stream, from which it follows that there must be a zone of upwelling between these two currents.

THE WIND SYSTEMS

Except in the entrance to the strait, the coastal winds are practically limited to two directions, prevailing north to northwesterly in summer, and south to

southeasterly in winter. Spring and autumn are periods of transition from one prevailing wind to the other. This is illustrated in figure 3 for a station outside the area directly concerned in the study, but the wind directions there are more representative of the conditions in the whole area than the observations from any of the shore stations which are located in Juan de Fuca strait.

Marmer showed that, with a southerly wind, the resultant component in the surface current was from 19 to 25 degrees to the right of the wind, that is, it flowed north to northeastward towards the Vancouver island shore. Northwesterly winds cause a current which deviates 21 to 33 degrees to the right of the wind, that is, the set of the current is south to southwestward, offshore.

The general depth of water in this area, except for a deep valley running

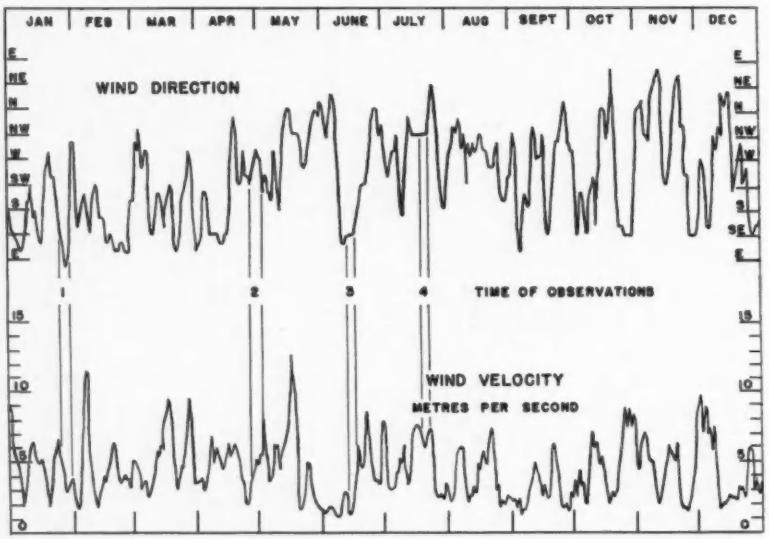

FIGURE 3. Daily average wind direction and velocity at Esteban point. The "Time of observation" indicates by vertical parallel lines when the data for each of figures 4, 5, 6, and 7 were obtained.

southwest from the entrance to the strait, is of the order of 100 to 150 metres which is about twice the depth of the influence of the majority of winds (Eckman 1928). From Eckman's calculations the steady state of the wind-driven currents should be attained in less than a day, and since there are from four to ten major changes of wind direction per month (fig. 3), each major wind has sufficient time to establish a steady current.

Particular care was taken to make the observations during periods of constant wind direction, and it may be assumed that only a single wind-driven current is represented in each diagram.

In general there is a wake stream flowing from Juan de Fuca strait into the ocean where there is a steady drift current. The current distribution is further

altered by the pressure gradient created between adjacent bodies of water, which may either accelerate or reduce the current or alter its direction.

It follows from the theoretical considerations that the wake stream must veer to the right, after leaving the strait, and approach the Vancouver island shore. During this travel it must absorb water from seaward, and eject it in the form of eddies along the shore, dissipating its energies and becoming broader in the process (Rossby 1936).

Since the wind-driven currents are either northwestward or southwestward, it is apparent that they must act either with (southerly winds) or against (northwesterly winds) the wake stream. The force of either current may vary, and, depending on the dynamic balance, a wide variety of current trajectories may result within these two types of circulation.

To illustrate the phenomena, four diagrams have been selected from a number made from various surveys. These represent the dynamic current field during typical seasonal states of the causative forces. The time and conditions under which the observations were made are indicated by vertical lines on figures 2 and 3. For instance, the winter observations were made during the last week in January.

Southeasterly Wind Effects

In this case the drift current and the wake stream were in conjunction. In a typical winter condition (fig. 4) when land drainage was at a minimum (fig. 2) and the prevailing winds were moderate southeast to easterly (fig. 3), the resulting drift current shows no evidence of wake stream influence, since the flow from the strait was too small to be effective. A series of eddies developed between the main current and the shore, which represented the water transported across the current. However it is noteworthy that there is no counter current within the limits of this survey, nor in any of several others made under these conditions. If this current was a true wake stream, a counter current would be indicated.

During early summer (fig. 6) when land drainage (fig. 2) was at a maximum, and the wind (figure 3) was moderate south to southeasterly, the wake stream had maximum force, and the drift current was very small. There was a well-developed stream from Juan de Fuca strait, which veered to the right around Swiftsure banks to cape Beale, where it encountered the land drainage waters from Barkley sound. The counter current was clearly indicated by the southward flow of the offshore water *against the wind*. Between these currents there occurred a region of maximum density indicating a zone of upwelling (stippled area in the figure).

There are many examples of this type of circulation on record illustrating various combinations of the drift current and wake stream, all of which are intermediate between these two examples.

Northwesterly Wind Effects

In this case (figs. 5 and 7) the drift current and wake stream were in opposition. The stream entered the ocean, proceeding on its theoretical course as long as its force was greater than the drift current. However, the force of this current was constantly being dissipated, whereas the drift current was being

accelerated, and it is evident that the wind current, no matter how weak, must eventually overpower the land drainage flow. When this occurred, the current veered to the left (seaward) and the drift current and the counter current acted in conjunction, with the result that the return flow (south and southeastward) was similar to, or greater than, the original stream flow.

It is apparent from the previous theoretical discussion of stream flow, that,

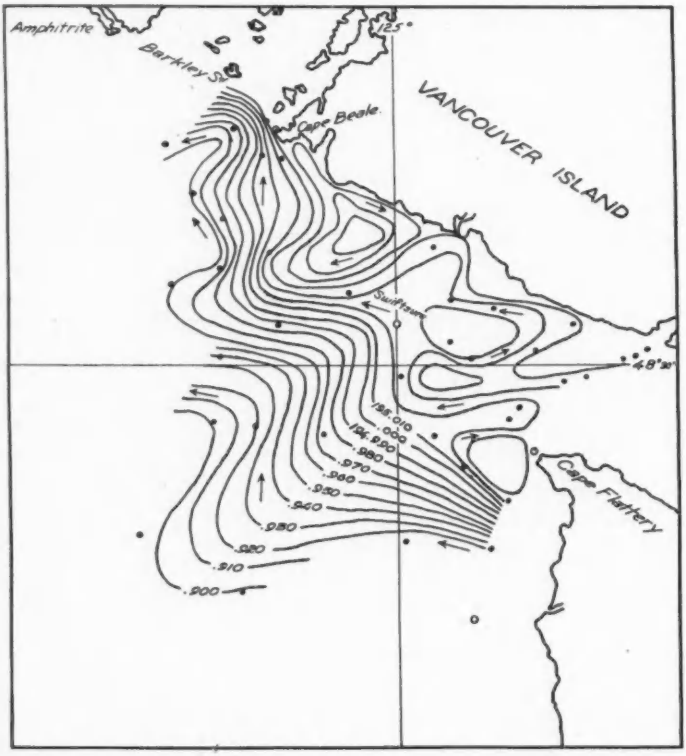

FIGURE 4. Calculated stream lines (pressure contours) in the approaches to Juan de Fuca strait in the winter during a period of small run-off and moderate southeast to easterly wind (1 in figs. 2 and 3). The black dots mark the positions of observations and the numbers (195.010, etc.) on the lines refer to their heights in dynamic metres above a base at 200 metres depth.

as the difference in velocity between these two opposing streams increases (the one being reckoned positive and the other negative), the intensity of upwelling must increase (since water is being transported out of the area between them) and the flow must become a cyclonic eddy (since each is being drawn into the other, cf. Bernouilli's theorem). The phenomenon is illustrated in these examples where the zone of upwelling (stippled) and the cyclonic eddy of high velocity were well developed.

During conditions of strong wake stream and northwesterly winds, this eddy and area of upwelled water are evident visually. At such times the surface water in the centre of the eddy is black, and may be as much as five degrees colder than the green water circulating around the eddy.

The south-flowing drift current carried brackish land-drainage waters from Barkley sound, which formed a sharp pressure gradient with the western (fig. 5)

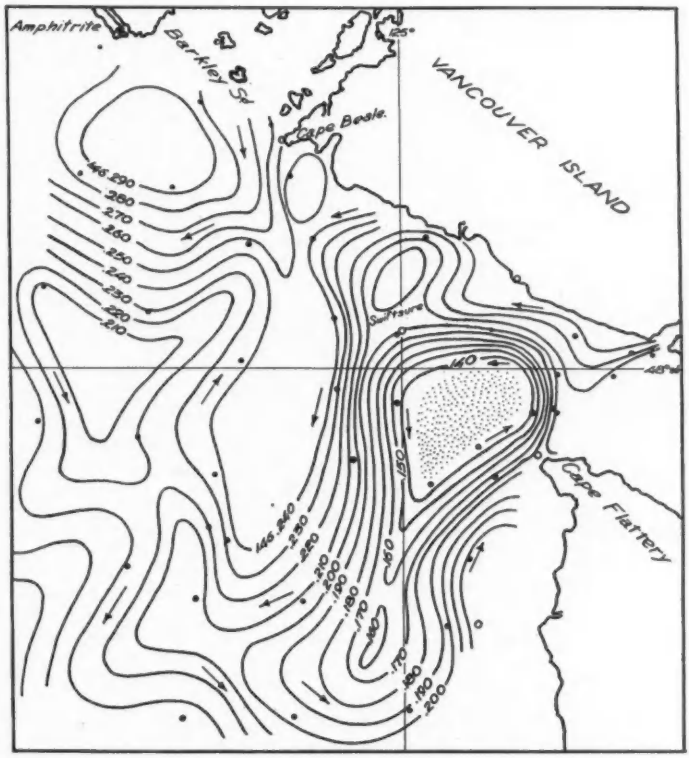

FIGURE 5. Calculated stream lines (pressure contours) in the approaches to Juan de Fuca strait in the spring during a period of average run-off and moderate westerly winds (2 in figs. 2 and 3). The black dots mark the positions of observations and the numbers (146.240, etc.) on the stream lines refer to their heights in dynamic metres above a base at 150 metres depth.

and northern (fig. 7) side of the wake stream flow, and so accelerated the current. This acceleration caused part of the current to veer again to the right for a short distance until it was overpowered by the drift current as shown in these examples.

During typical spring conditions (fig. 5) when the run-off was less than average, and the northwesterly wind was well established, the wake stream was over-

powered before it reached Swiftsure banks and a very rapid eddy circulation set up around a well-developed centre of upwelling.

During late summer (fig. 7) when land drainage was greater than average, and the northwesterly wind was about the same as represented in figure 5, the stream flow was much stronger than before, persisting intact as far as Barkley sound where it gained distinct regeneration from the land drainage waters. The

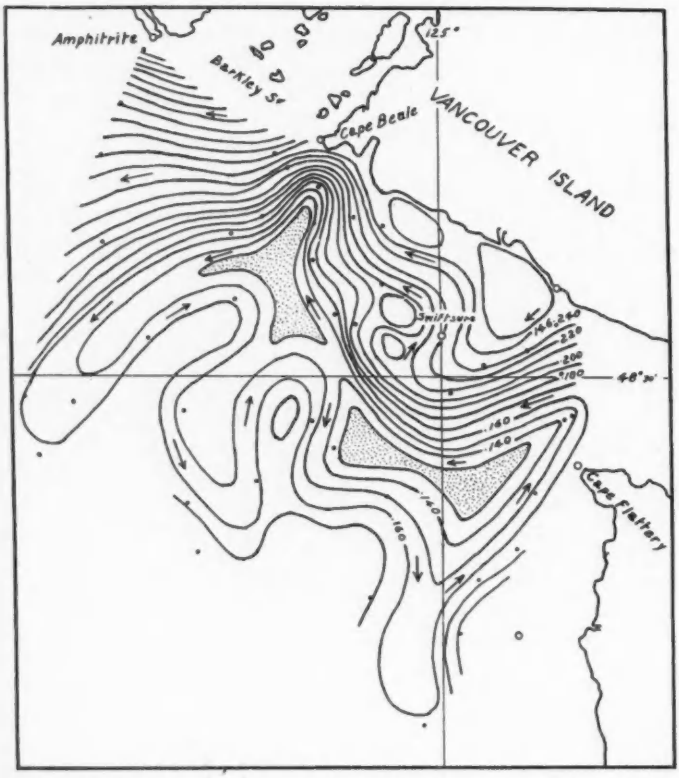

FIGURE 6. Calculated stream lines (pressure contours) in the approaches to Juan de Fuca strait in the early summer during a period of maximum run-off and moderate southeast to easterly winds (3 in figs. 2 and 3). The black dots mark the positions of observations, and the numbers (146.240, etc.) on the stream lines refer to their heights in dynamic metres above a base at 150 metres depth.

zone of upwelling was further to seaward than before (fig. 5), and the velocity around the eddy was not so rapid. But the return current was of the same order of magnitude as the wake stream.

DISCUSSION

It is evident from these few illustrations that the non-tidal flow in the entrance to Juan de Fuca strait is essentially a resultant of the force of the wake

stream from the strait and of the direction and force of the coastal drift currents modified by the gradients between the water masses. During southeast winds the flow is wide, continuous, and northwestwards parallel to the Vancouver island coast. A large eddy may be formed between the seaward side of the wake stream and the counter current, if land drainage is at a maximum and the wind force is small, but the return velocity in such a case is never as great as the wake stream

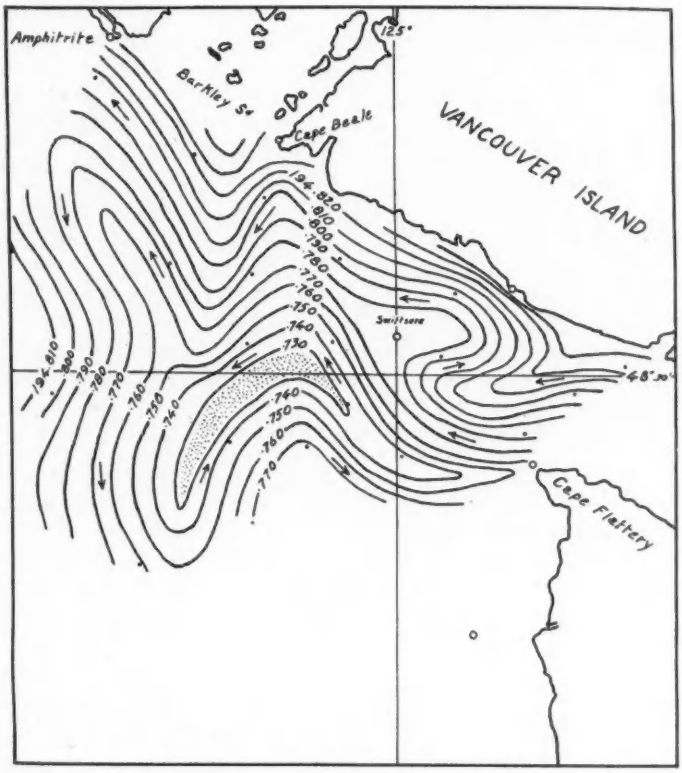

FIGURE 7. Calculated stream lines (pressure contours) in the approaches to Juan de Fuca strait in the late summer during a period of slightly greater than average run-off and fresh northwesterly winds (4 in figs. 2 and 3). The black dots mark the positions of the observations, and the numbers (194.820, etc.) on the stream lines refer to their heights in dynamic metres above a base at 200 metres depth.

velocity. During northwesterly winds, a large cyclonic eddy is formed, owing to the reaction of the wake stream and the drift current, and the velocities on all sides of the eddy are of the same order of magnitude.

With increasing strength of flow from Juan de Fuca strait, the resultant current flows further and further to seaward before veering towards the right. When the flow is at a minimum, the current follows the Vancouver island coast

closely; when it is at a maximum, the wake stream passes well to the westward of Swiftsure banks and an area of eddies occurs between the stream and the shore. When this current is opposed by the wind, the distance of the centre of the characteristic cyclonic eddy from the shore becomes greater with the strength of the stream.

It is of interest to note, that in all of these diagrams the general set of the surface current is northwestward from Juan de Fuca strait to cape Beale. This phenomenon was first indicated on the Admiralty charts of the area as early as 1853, and has subsequently been discussed by Marmer (1926), who concludes (parts marked with * inserted by author):

"It is obvious that the fresh water from the territory that the Strait of Juan de Fuca drains must be a large factor in the nontidal current at Swiftsure Bank Light Vessel . . . . the direction of the current is seen to be westerly (northwesterly)* every month. For the entire period of the observations the nontidal current averaged 0.47 knots, setting 316°, or almost due northwest, and for every month of this period the nontidal current averaged northwesterly with a single exception of June, 1915, for which month . . . . (the direction was)* 7° south of west."

(Compare with fig. 5.)

"The velocity of the nontidal current appears to be greatest during the fall and winter months and least during spring and summer. This variation can not be ascribed to changes in the volume of the drainage waters setting seawards, for the fresh-water discharge of the streams draining into the Strait of Juan de Fuca is least during the fall months. It appears to be due, however, to the winds which here are prevailingly from the east (mag.; south to southeast, true)* during fall and winter and from the west (mag.; northwest to north or southwest, true)* during spring and summer."

Marmer's conclusion that the non-tidal currents at Swiftsure lightvessel appeared to be greatest during periods of southeast winds, and least during northwesterly winds agrees with the observations made. In the first case the winds are in conjunction with the wake stream and in the latter case they oppose it. However his suggestion that the strength of the current is seasonal is open to question.

The strength of the wake stream is seasonal (fig. 2), and a greater proportion of the winds oppose the wake stream during summer than during winter (fig. 3). But it is not necessarily a consequence that the strength of the total current at Swiftsure is a seasonal function since there are many northwesterly winds during autumn and winter, and many southeasterly during spring and summer.

In each of the diagrams there is at least one zone of strong currents, and in each case this zone is of a different, though related, form and in a different position. As mentioned before, the strength of the current appears further to seaward as the strength of the wake stream increases. It is thus evident that observations from a fixed point, such as Swiftsure lightvessel, would only indicate the maximum currents in the area, if these occurred at the point of observation.

The greatest velocity of flow would be expected to occur during the period of maximum land drainage when the winds were southeasterly. Such a case has been observed and it was indicated that the maximum non-tidal current in the area was of the order of five knots, but in this instance Swiftsure lightvessel lay

in the area of eddies on the right-hand side of the stream, where a relatively weak current was observed.

The minimum velocity was observed during the late autumn when land drainage was at a minimum and northwesterly winds were strong. Under these conditions the southward set offshore was the main current and the northwestwards set along the shore was in reality a counter current and relatively weak. Swiftsure was in the path of the counter current and could not experience the strong offshore set.

From the principles that have been enunciated it is possible to deduce the probable general form of the current fields in the area under different conditions, with less mental confusion than if they were described.

In connection with the northwestward set along the Vancouver island shore, it is interesting that this coast has been designated the "Graveyard of the Pacific", owing to the large number of ships that have been wrecked on the part of the Vancouver island coast that adjoins this area. During the latter part of the last century, when sea transport was largely by sailing ship or low-powered vessels, it was customary to wait outside Juan de Fuca strait for a tug, or clear weather, or until daylight. Owing to lack of navigational aids, the rate of drift of the ship could not be determined at night or during fog, and unknowingly the ship would be set strongly towards the shore, as indicated in the figures, where it would be endangered by outlying reefs.

ACKNOWLEDGEMENTS

The author wishes to make acknowledgement to the Lighthouse and Meteorological services of the Department of Transport, and the Dominion Water Power and Hydrometric Bureau of the Department of the Interior, Dominion of Canada, for the data shown in figures 2 and 3. Particular thanks are due to Commander H. W. S. Soulsby, the officers and men of H.M.C.S. *Armentieres* for their help in conducting the dynamic surveys of the area, and to Messrs. W. Anderson, H. J. Hollister and R. Fjarlie, for their assistance in making the observations and later carrying out the tedious preparations of the data for presentation.

REFERENCES

ECKMAN, V. W. *J. Conseil*, **3** (3) 295-325, 1928.

HELLAND-HANSEN, B. The Sognefjord section. James Johnstone Memorial Volume, University Press of Liverpool, pp. 257-274, 1934.

MARMER, H. A. *U.S. Coast Geodetic Surv., Spec. Pub.* **121**, 63-77, 1926.

PARR, A. E. *J. Mar. Res.*, **1** (2), 119-132, 1938.

ROSSBY, C.-G., AND COLLABORATORS. *Bull. Amer. Meteor. Soc.* **18**, 201-209, 1937.
Pap. Phys. Oceanog. Meteor. Mass. Inst. Tech. and *Woods Hole Oceanog. Inst.* **5**, 1-43, 1936.
J. Mar. Res. **1**, 1, 15-27, 1938.

SMITH, E. H. *U.S. Coast Guard Bull.*, **14**, 1-50, 1926.

SPILHAUS, A. F. *J. Mar. Res.*, **1**, 1, 29-33, 1938.